

David L. Hawksworth
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Editors

TOPICS IN BIODIVERSITY AND CONSERVATION



Biodiversity and Conservation in Europe



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Biodiversity and Conservation in Europe

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Biodiversity and Conservation in Europe

Edited by

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and

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Introduction

Biodiversity and Conservation in Europe

This issue brings together a selection of original studies submitted to *Biodiversity and Conservation* addressing aspects of the conservation of biodiversity in Europe. Europe is the most intensively studied area of the world with respect to its biota, and in many of its countries active conservation and recording programmes are well-established. In addition there have been transnational and concerted actions across countries of the European Economic Community (EEC) to address conservation issues. At the same time these actions are being taken in a continent subjected to an almost unparalleled amount of human disturbance and industrial development. The European experience can therefore serve as a model and provide lessons for what might be achievable in other continents and countries if there is sufficient political and public will, and the necessary resources are made available.

The 28 papers included here represent a wide spectrum of groups of organisms and issues concerning their conservation. The organisms covered include wild-fowl, waterbirds, steppe birds, golden and booted eagles, terns, Iberian ibex, Arctic fox, small mammals, rabbits, amphibians and reptiles, lizards, loggerhead turtles, butterflies, spiders, field crickets, centipedes, stream macroinvertebrates, oribatid mites, plants, bryophytes, lichens, and truffles. The multifarious factors affecting European wildlife are represented here by modifications of calcareous grasslands, changes in forestry practices, fire, agricultural effects on wetlands, grazing, hunting, and wind turbines. Also discussed are attitudes of forest managers, sociological constraints, and buffer areas. The tools available for use in conservation assessments and monitoring utilized include public databases, indices, modelling, radio tagging, niche factor analysis, and a vulnerability index. The papers involve studies conducted Europe-wide or from particular countries, notably Belgium, France, Germany, Italy, The Netherlands, Norway, Slovakia, Spain, and the UK.

This diverse series of studies presented together here, provides an indication of current research activities taking place in Europe that will be of value to students undertaking courses in aspects of biodiversity and conservation. They can be viewed as a series of topical case-studies that will expose students to a selection of the types of primary research and conservation actions being conducted now in

the continent. As such they will complement the necessarily less-detailed specific information available in textbooks and secondary review articles.

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Biodiversity gradients in the Alps: the overriding importance of elevation

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Abstract Land abandonment is causing woodland expansion and loss of open habitats in the Alps, coupled with a shift in forestry practices from coppice management to high forest. Despite such rapid large-scale changes, there has been very little investigation of the environmental predictors of biodiversity in the Alpine landscape. We assessed the richness of amphibians, reptiles and breeding birds ($n = 189$ species), used as a surrogate of biodiversity, in 58 quadrats of 100 km^2 , located within a well surveyed area of the province of Trento (central-eastern Italian Alps). The surrogates were then related to a series of environmental variables by means of stepwise multiple regression. Depending on the surrogate analysed, species richness declined linearly or quadratically with elevation, and increased with habitat heterogeneity and the availability of grassland and arid-rocky habitats. The same results were obtained when incorporating a measure of species threat into the biodiversity estimates. Different surrogates were positively inter-correlated, probably because of a common response to the same factor, namely elevation, which was the only variable to enter all models. Such elevational gradient produced a clear biodiversity peak in low-elevation areas, generating potential conflict between efficient biodiversity conservation and economic interests linked to human development, a scenario which probably applies to many mountain regions worldwide. The current network of protected areas was quite satisfactory in terms of area covered but biased towards high-elevation areas, of high scenic beauty but relatively low in animal biodiversity value. Low-elevation reserves were small and isolated. Proposed conservation targets include the establishment of corridors increasing the connectivity of low-elevation reserves and the promotion of incentives for the extensive management of grassland, an agro-ecosystem of high historical and biological value.

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Keywords Alps · Biodiversity · Elevation · Grassland · Habitat heterogeneity · Protected areas · Reserve network · Species richness · Vertebrates

Introduction

In recent decades, the worldwide rapid loss of biodiversity has promoted new approaches to conservation, with two main emergent trends. Firstly, the traditional focus on single species conservation has been increasingly questioned and replaced with broader biodiversity-driven targets (e.g. Franklin 1993; Tucker and Evans 1997; Entwistle and Dunstone 2000). Secondly, there is increasing consensus that, for biodiversity preservation to be effective, the establishment of protected areas should be more integrated with the maintenance of hospitable environments within the unprotected matrix of managed landscapes (e.g. Shafer 1994; White et al. 1997; Norris and Pain 2002). This is especially important considering that land-use practices have been identified as the single major cause of biodiversity loss in recent years (Soulé 1991). The above cited trends have caused a high interest in databases reporting biodiversity estimates over large areas. In this context, atlas data on species distribution have become a valuable tool to derive spatial estimates of species richness (frequently employed as a surrogate of biodiversity, Purvis and Hector 2000) subsequently used for conservation planning (e.g. Boone and Krohn 2000; Wessels et al. 2000; Underhill and Gibbons 2002).

In Europe, the Alps represent a large expanse of natural and semi-natural habitats, which may function as important sources of colonizers for the surrounding intensively cultivated lowlands. Despite such strategic importance and the fact that mountain systems are generally regarded as hotspots of biodiversity (Lomolino 2001; Körner and Spehn 2003), the alpine landscape is currently going through a series of profound changes with unknown biodiversity consequences. Firstly, as in other mountainous areas of Europe, the declining profitability of agro-pastoral activities is causing widespread land abandonment, with consequent woodland expansion into previously cultivated areas (Cernusca et al. 1999) and negative impacts on species of open habitats (e.g. Laiolo et al. 2004). In particular, woodland extent is increasing through natural regeneration by 0.5–1% per year, almost exclusively at the expense of abandoned pastures (e.g. PAT 1995; Barbaro et al. 2001; CIPRA 2001; Dirnböck et al. 2003). Such change can be decomposed into two simultaneous processes: (1) at medium-low elevations, land abandonment causes the loss of grassland fields originally managed for fodder production in association with the once flourishing livestock industry, an agro-pastoral system which dates back to 6,000 years ago (Lichtenbergen 1994; Dirnböck et al. 2003); (2) at higher elevations, the rapidly declining utilization of alpine pastures for livestock rearing is causing an upward shift of the tree-line, originally lowered by human action so as to increase the surface available for grazing (Dirnböck et al. 2003). Both processes promote a temporary increase in shrub vegetation, which ultimately develops into woodland, leading to long-term loss of alpine grassland and pastures, and declines in landscape heterogeneity. Secondly, the above cited woodland expansion is accompanied by a rapid change in forestry practices. Much of the low-elevation broadleaved woodland, once managed by stool-shoot regeneration (coppice management, Matthews 1989), is being converted to high forest, a process favoured by incentives from local administrations and from the Common Agricultural Policy of the European Union (e.g. IPLA 2000). Such radical, large-scale changes impose an urgent need for investigations of their potential biodiversity impact. To date, there has been few comprehensive investigations of the potential landscape-level determinants of biodiversity in the Alpine

chain, most of the studies focusing on “restricted” groups of species in specific components of the landscape (e.g. birds in grassland habitats, Laiolo et al. 2004).

Here, we: (1) assess the richness of terrestrial vertebrate species in an area of the central-eastern Italian Alps; (2) investigate the potential environmental predictors of biodiversity level; (3) examine the inter-correlation among different biodiversity estimates; (4) assess the potential biodiversity impact of the ongoing landscape changes; (5) identify hotspots of vertebrate diversity and compare them with the location of the local reserve network; and (6) propose conservation guidelines aimed at the long-term preservation of biodiversity in the modern alpine landscape.

Methods

Study area

Vertebrate species were surveyed in a 6,300 km² plot coinciding with the administrative province of Trento, located in the central-eastern Italian Alps (45° N, 11° E, Fig. 1). Elevation of the study area ranged from 65 to 3764 m a.s.l. Thirty-one percent of the land lay below 1,000 m, twenty-eight percent at an elevation between 1,000 and 1,500 m, 22% between 1,500 and 2,000 m, 13% between 2,000 and 2,500 m, and 6% at an elevation >2,500 m. The natural tree line is at 1,800–1,900 m, but has often been lowered by human activities and sheep grazing. The landscape is characterized by intensively cultivated valley floors, mountain slopes covered by forests interspersed with sparse pastures and vineyards at lower elevation, by managed grassland at middle elevation, and by montane grassland, rocky outcrops and permanently snow-covered ground above the tree line. In particular, 52% of the area was covered by woodland, 18% by montane grassland and pastures, 6% by

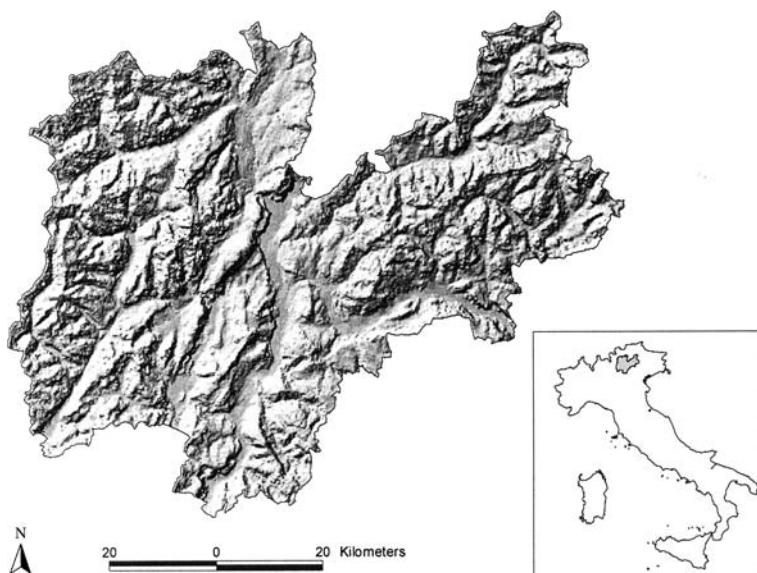


Fig. 1 Relief map of the Administrative Province of Trento. The inset shows the location of the study area in the Italian peninsula

agricultural crops (mainly vineyards and apple groves) and 3% by human development (GIS analysis on CEC 1993). Forest composition varied from deciduous to coniferous depending on elevation, slope orientation, and local microclimate. With increasing elevation, woodland tended to be dominated respectively by *Quercus pubescens*, *Quercus-Tilia-Acer* spp., *Fagus-Abies* spp., *Picea excelsa* and *Larix decidua-Pinus cembra* (PAT 1995). Eighty-two percent of the woodland area was managed for wood production; 73% of this woodland was managed as high forest and 27% as coppice (PAT 1995). The network of protected areas is composed of three large parks (Stelvio National Park, Adamello-Brenta Regional Park and Paneveggio-Pale di San Martino Natural Park) and by 65 smaller reserves (“biotopi provinciali”, PAT 1997) (Fig. 3).

Distributional data

The distribution of terrestrial vertebrate species has been recorded in the study area since 1987, as part of different atlas projects (Caldonazzi et al. 2002; Pedrini et al. 2005), and expressed as the presence-absence of each species in the $10\text{ km} \times 10\text{ km}$ quadrats of the national 1:25000 cartography. Intensive field surveys were conducted year-round between 1987 and 1996. The data collected in this period showed that species richness increased linearly with sampling effort, reaching a plateau above 20–25 visits per quadrat. Therefore, between 1996 and 2001, under-sampled quadrats were surveyed until all quadrats had received a minimum of 25 visits. Further details on field procedures can be found in Caldonazzi et al. (2002) and Pedrini et al. (2005). For the purpose of this study, we only included in the analyses the quadrats which were included for $\geq 85\%$ of their surface in the study area ($n = 58$ quadrats), so as to avoid the potential sampling biases associated with area-effects (Gaston 1996a). For these 58 quadrats, none of the biodiversity estimates was significantly related to the percentage of each quadrat included in the Trento administrative province ($r \leq 0.16$, $P \geq 0.24$).

Statistical and GIS analyses

To investigate the potential effect of environmental factors on biodiversity, for each quadrat we: (1) calculated the richness of amphibian, reptile and avian species and their cumulated richness (hereafter “vertebrate richness”), and used them as surrogate measures of biodiversity (Table 1); (2) measured the environmental variables reported in Table 1 by accessing GIS land-use maps (CEC 1993; Servizio Foreste 1999) or by digitising 1 m-resolution, aerial colour-photographs (courtesy of Provincia Autonoma di Trento, “Permit IGM n.278 of 30 June 2000”); and (3) employed stepwise multiple regression with a generalised linear model procedure (GLM, Crawley 1993) to relate the biodiversity estimates to the environmental variables of Table 1. Because high species richness does not necessarily equate to high conservation priority or level of threat (Gaston 1996b), we also calculated for each quadrat the richness of bird species classified as vulnerable by Tucker and Heath (1994) (i.e. cumulative richness of species classified as SPEC 1, 2, and 3; Table 1), and employed it as a dependent variable in an additional multiple regression. No similar analysis was conducted for amphibians and reptiles because the vulnerability status of such species is less known.

In all regressions, we added to the set of explanatory variables a quadratic term for elevation (calculated on the untransformed variable), because species richness was shown to peak at intermediate elevations in some previous studies (Rahbek 1997; Brown 2001). No direct estimates of climate could be included among the explanatory variables because of a

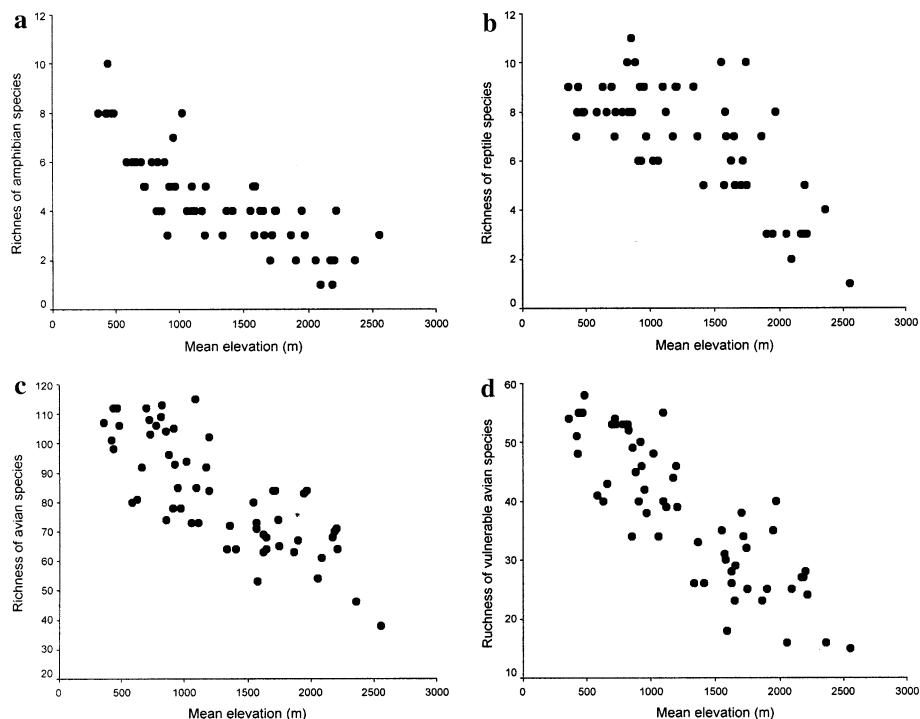


Fig. 2 Elevational decline in species richness for amphibians (a), reptiles (b), birds (c) and vulnerable birds (d)

low number of weather-recording stations with long-enough time-series. However, we assigned each quadrat to a climate-category reflecting the climatic zonation proposed by Odasso (2002) on the basis of soil characteristics and phytosociological community type (Table 1). Furthermore, climate can be adequately estimated through topographical surrogates (e.g. elevation) when: (1) the extent of the study area is relatively small; (2) climate remains relatively constant over the study area; and (3) the lapse rate of temperature with increasing elevation is constant through the study plot (Gandolfo and Sulli 1993; Austin 2002). The three conditions apply to this study.

All multiple regressions (GLMs with Poisson errors and a logarithmic link function) were built by a backward stepwise procedure following Crawley (1993): all explanatory variables were fitted to the model, extracted one at a time from such maximal model and the associated change in model deviance assessed by a χ^2 test. Overdispersion was checked following Crawley (1993). To reduce collinearity and the number of variables presented to the multivariate models, we employed a modification of the method of variable reduction proposed by Green (1979) and commonly employed in habitat selection studies (e.g. Austin et al. 1996; Sergio and Bogliani 2000; Sergio et al. 2004 and references therein). In this method, pairs of strongly intercorrelated, explanatory variables ($r > 0.6$) are considered as estimates of one underlying factor. Only one of the two is retained for analysis, usually the one considered as more biologically relevant in terms of the investigated relationship. Of the remaining variables, only those that were significantly related to the dependent variable in univariate correlations were retained as explanatory variables.

The relationship among different biodiversity surrogates was assessed by means of univariate correlations (Sokal and Rohlf 1981). To examine whether the current network of

Table 1 Biodiversity estimates and environmental variables measured at 58 quadrats of 100 km² (Trento region, central-eastern Italian Alps)

| Variable | Description |
|--------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------|
| <i>Biodiversity estimates</i> | |
| Richness of amphibians | Number of amphibian species recorded as present in the quadrat |
| Richness of reptiles | Number of reptile species recorded as present in the quadrat |
| Richness of birds | Number of bird species recorded as present in the quadrat |
| Richness of vertebrates | Cumulative number of amphibian, reptile and bird species in the quadrat |
| Richness of SPEC 1–4 | Number of vulnerable ^a bird species recorded as present in the quadrat |
| <i>Environmental variables</i> | |
| Mean elevation (m) | Mean elevation within the quadrat ^b |
| Range of elevation (m) | Range of elevation within the quadrat ^b |
| Mean slope | Mean slope angle within the quadrat ^b |
| Mean ruggedness index | Mean of the ruggedness indices ^c of each of all the 1-km ² quadrats included within the 100-km ² quadrat |
| % urban | % extent of urban areas ^d |
| % grassland | % extent of managed grassland ^d |
| % alpine pastures | % extent of alpine grassland above the tree line ^d |
| % vineyards | % extent of vineyards ^d |
| % apple groves | % extent of apple groves ^d |
| % farmland | % extent of intensive farmland (excluding vineyards and apple groves) ^d |
| % arid | % extent of rocky outcrops and xerophytic vegetation ^d |
| % shrubs | % extent of shrubs ^d |
| % shrubs in evolution | % extent of shrubs evolving into woodland vegetation after land abandonment ^d |
| % broadleaved forest | % extent of broadleaved forests ^d |
| % conifer forest | % extent of conifer forests ^d |
| % mixed forests | % extent of mixed broadleaved and conifer forests ^d |
| % water | % extent of aquatic habitats ^d |
| % roads | % extent of the road-network ^{d,e} |
| % total grassland | Sum of: % grassland + % alpine pastures |
| % total farmland | Sum of: % vineyards + % apple groves + % farmland |
| % total shrubs | Sum of: % shrubs + % shrubs in evolution |
| % total woodland | % extent of woodland ^d |
| % coppice woodland | % extent of coppice-managed woodland ^f |
| % high forest | % extent of mature forest ^f |
| River length (km) | Length of rivers ^f |
| No. of wetlands | Number of wetlands (<0.5 ha) ^g |
| Habitat diversity | Shannon index of land-use diversity (Krebs 1998) |
| Phyto-climatic factor | Dichotomic factor discriminating between warm, dry sites on carbonatic soils (1) and other areas (2) (based on the zonation by Odasso 2002) |

^a Species classified as SPEC 1, SPEC 2 or SPEC 3 by Tucker and Heath (1994)

^b Calculated from a 10 m-resolution digital elevation model

^c Number of 10-m contour lines crossed by two N–S and W–E transects of 1 km, crossing in the centre of the 1-km² quadrat

^d Recorded by accessing GIS land-use maps (CEC 1993) and, when necessary, by digitising 1 m-resolution, aerial colour-photographs

^e Assuming a 10-m buffer along all asphalted roads

^f Recorded by accessing GIS land-use maps (Servizio Foreste 1999) or by digitising 1 m-resolution, aerial colour-photographs

^g Digitised from 1 m-resolution, aerial colour-photographs

protected areas is efficient at preserving biodiversity, we: (1) defined as biodiversity hot-spots the 12 quadrats in the upper quintile of the values of vertebrate richness (Harcourt 2000) and compared their distribution with the location of the main local reserves; and (2) used univariate correlations to relate the biodiversity surrogates to the percentage of each quadrat which was under some sort of protection. Means are given ± 1 SE, tests are two-tailed, and statistical significance was set at a $\alpha \leq 0.05$. Prior to parametric tests, variables were logarithmically, square-root or arcsin square-root transformed as necessary in order to achieve a normal distribution or normalise the standardised residuals or multiple regressions. When multiple tests were performed on the same data set, the sequential Bonferroni correction was used to adjust the significance level (Rice 1989).

Results

Richness of amphibian, reptile and bird species

Data were available for 13 amphibian species, 12 reptile species and 164 avian species. The richness of amphibian species was only related, linearly, to elevation (Table 2a, Fig. 2a). The richness of reptile species showed a quadratic decline with increasing elevation

Table 2 Effect of environmental variables on the richness of vertebrate species recorded in 58 quadrats of 100 km² (Trento region, central-eastern Italian Alps)

| Variable | Parameter estimate \pm SE | χ^2 | P | % deviance explained |
|------------------------------------------------------------|-----------------------------|----------|--------|----------------------|
| (a) Effect on: richness of amphibian species ^a | | | | 65.5 |
| Mean elevation | -0.051 ± 0.004 | 10.31 | <0.01 | |
| Constant | 2.894 ± 0.205 | – | – | |
| (b) Effect on: richness of reptile species | | | | 59.2 |
| Mean elevation | 0.003 ± 0.002 | 1.70 | >0.05 | |
| Mean elevation ² | -0.002 ± 0.000 | 8.10 | <0.02 | |
| Constant | 7.325 ± 1.050 | – | – | |
| (c) Effect on: richness of bird species | | | | 63.6 |
| Mean elevation | -0.022 ± 0.023 | 0.98 | >0.05 | |
| Mean elevation ² | -0.015 ± 0.001 | 9.10 | <0.01 | |
| Habitat diversity | 1.287 ± 0.138 | 8.88 | <0.01 | |
| Constant | -52.63 ± 57.53 | – | – | |
| (d) Effect on: richness of vertebrate species ^b | | | | 75.0 |
| Mean elevation | -0.011 ± 0.007 | 1.83 | >0.05 | |
| Mean elevation ² | -0.002 ± 0.001 | 10.71 | <0.01 | |
| % total grassland ^c | 0.377 ± 0.177 | 5.84 | <0.05 | |
| % arid ^d | 0.591 ± 0.153 | 11.21 | <0.001 | |
| Constant | 6.182 ± 0.291 | – | – | |
| (e) Effect on: richness of vulnerable bird species | | | | 73.4 |
| Mean elevation | -0.037 ± 0.032 | 3.78 | <0.05 | |
| Mean elevation ² | -0.025 ± 0.011 | 6.48 | <0.05 | |
| % total grassland ^c | 0.882 ± 0.123 | 7.30 | <0.02 | |
| % arid ^c | 0.812 ± 0.224 | 8.32 | <0.001 | |
| Constant | 7.311 ± 0.221 | – | – | |

^a Variable log_e transformed

^b Cumulative richness of amphibians, reptiles and bird species

^c Variable arcsin square-root transformed

(Table 2b, Fig. 2b). The richness of bird species declined quadratically with elevation and increased with habitat heterogeneity (Table 2c, Fig. 2c). The richness of all vertebrate species showed a quadratic response to elevation and increased with the availability of grassland and arid-rocky habitats (Table 2d). The same variables entered the model with the richness of vulnerable bird species as the dependent variable (Table 2e, Fig. 2d).

Inter-correlation among biodiversity surrogates

The inter-correlation among the richness of amphibians, reptiles and birds was positive and significant in all cases ($r \geq 0.60$, $n = 58$, $P \leq 0.0001$). The richness of the three vertebrate classes was also positively correlated with the richness of vulnerable bird species (in all cases $r \geq 0.62$, $n = 58$, $P \leq 0.0001$). Finally, the richness of vulnerable bird species was positively correlated with the richness of non-vulnerable bird species ($r = 0.85$, $n = 58$, $P < 0.00001$).

Biodiversity hotspots and the protected area network

All the 12 quadrats identified as hotspots were located along the main valley floors of the region (Fig. 3), as to be expected on the basis of the results outlined above. Most of the quadrats were poorly protected (Fig. 3). The percentage of each quadrat included in any type of protected area increased with the mean elevation of the quadrat ($r = 0.37$, $n = 58$,

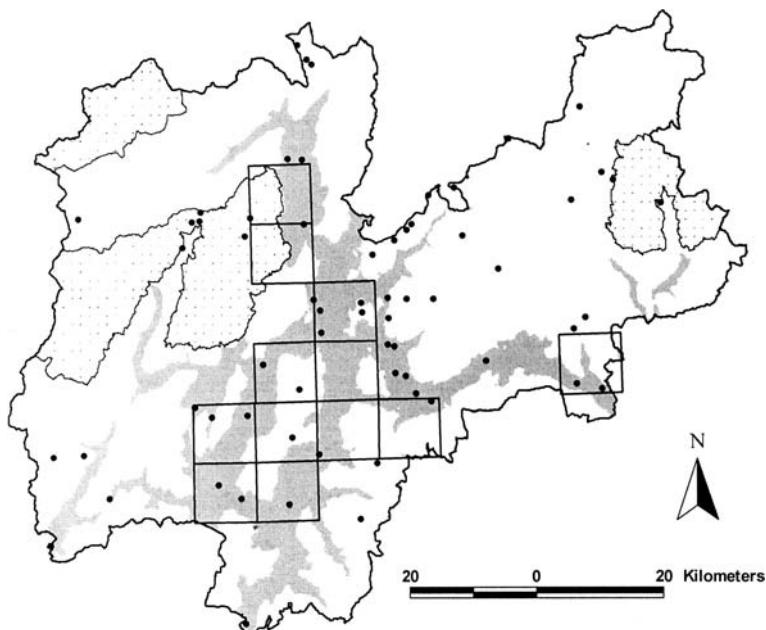


Fig. 3 Biodiversity hotspots and protected areas in the Trento region of the central-eastern Italian Alps. The stippled polygons represent the three large parks of the region (Stelvio, Adamello-Brenta and Paneveggio-Pale di San Martino), the black points represent the “biotopi provinciali” (smaller reserves). Grey patches depict areas below 800 m of elevation and the large quadrats are the 12 hotspots identified in our dataset on the basis of the cumulative richness of all vertebrate species (see Methods)

$P = 0.03$) and was negatively related to all the biodiversity surrogates (all $r \leq -0.18$), though only the relationship with reptiles was significant ($r = -0.33$, $n = 58$, $P = 0.05$).

Discussion

The richness of the vertebrate species employed in this study was related to elevation, habitat heterogeneity and the availability of two land-cover types. At the spatial scale analysed, topography, elevation in particular, was the single most important variable, entering all models and explaining alone a large part of the variation in species richness, as commonly reported in previous studies (review in Gaston and Williams 1996). In agreement with recent reviews (Rahbek 1997; Gaston and Williams 1996; Brown 2001), species richness declined both linearly or quadratically with elevation, depending on the taxa considered. In contrast, we did not observe the biodiversity peak at medium elevations reported by some authors (e.g. Brown 2001), the richness estimates usually declining steadily, though curvilinearly, all along the elevation gradient (Fig. 2). The biodiversity decline with increasing elevation is probably caused by three non-exclusive factors. Firstly, climate becomes progressively colder with increasing elevation, temperature usually declining at a lapse rate of $7^{\circ}\text{C}/\text{Km}$ increase in elevation (Wallace and Hobbs 1977; Beniston 1994). The lower temperature at higher elevation, frequently accompanied by higher rainfall and snow cover, results in a progressively more hostile and less energy-rich environment for most species, thus promoting the decline in species richness (e.g. Boone and Krohn 2000). Secondly, the elevational biodiversity decline may be an area-effect related to the three dimensional surface-decline with increasing elevation typical of mountain systems (Gaston and Williams 1996; Lomolino 2001). The increase in species richness with available area is a long recognized pattern in ecology (species-area curve, review in Rosenzweig 1995). Thirdly, the above cited larger area, more favourable climate and higher available energy at lower elevations may promote high habitat heterogeneity, which is often a direct determinant of species richness (e.g. Owen 1990; Lomolino 2001). In our study, the first explanation (climate-driven elevational decline in species richness) was supported by the fact that ectothermic species seemed to respond solely to elevation while endothermic species responded to elevation as well as to other factors.

Besides the effect of elevation, bird richness was also positively related to habitat diversity. A higher availability of different habitat types probably implies a higher number of potential niches, ultimately promoting higher species richness (Hutchings et al. 2000; Tilman 2000). A similar relationship has been reported in other previous studies (e.g. Miller 1994; review in Gaston 1996b; Hansen and Rotella 1999) and habitat diversity has even been proposed as a surrogate of biodiversity (reviews in Wessels et al. 1999; Margules and Pressey 2000; Purvis and Hector 2000).

Finally, the richness of all vertebrates and of vulnerable bird species was positively related to the availability of grassland and of arid and rocky habitats. Extensive agro-ecosystems are well known for their biological richness and many species are strictly dependent on such habitats in the Alps (e.g. Pain and Pienkowski 1997; Tucker and Evans 1997; Laiolo et al. 2004). Arid habitats are frequently located in sites with a rugged topography, scarce human access and alteration, and often show particularly warm micro-climates, thus favouring the persistence of many “Mediterranean” species typical of warmer areas (e.g. Marchesi and Sergio 2005). In a way, grassland and arid patches are frequently the main features which stand out of the regional woodland matrix, thus providing an essential contribution to landscape heterogeneity (Forman 1995).

Conservation implications

The positive inter-correlation among the different biodiversity surrogates, including those incorporating a measure of species vulnerability, simplifies any prioritisation strategy because sites with high species richness for one taxon will also show high richness for other taxa. Such spatial concordance was probably promoted by the common response of all the taxa analysed to the local elevational gradients, as confirmed by the fact that the inter-correlation among the surrogates disappeared when controlling for the effect of elevation through a partial correlation analysis (all $r \leq 0.17$, $P \geq 0.22$). On the contrary, the biodiversity peak at low elevation may generate conflict between the implementation of efficient conservation and human development, which also peaks at low elevation. In particular, the current reserve network in the Trento region is dominated by three large parks and a series of smaller “biotopi” (Fig. 3). The three parks cover almost exclusively high elevation areas (Fig. 3), while most of the biotopi-reserves coincide with low elevation wetlands, but, despite their obvious value, their size is always too small to allow the persistence of most vertebrate species (mean area = $0.51 \pm 0.07 \text{ km}^2$, $n = 65$). Therefore, the system is characterized by a relatively satisfactory amount of protected land (17% of the area), but also by a bias towards the preservation of unproductive, high-elevation, biodiversity “poor” sites, a condition which typifies many developed countries (e.g. Sutherland 1998; Margules and Pressey 2000). Considering that the economic value of the lowlands for agriculture and for urban development makes the planning of large lowland reserves unrealistic, a more rewarding conservation strategy could focus on two targets: (a) utilize the biotopi-reserves as stepping stones and attempt to connect them through corridors; and (b) strive to make the unprotected matrix of the lowlands as hospitable as possible for wildlife. The above scenario is likely to be common to many mountain systems worldwide (see Hansen et al. 1999 for similar conflicts).

As for the habitat changes currently occurring in the alpine landscape, our results suggest that forest expansion per se and the conversion of coppice woodland to high forest may not be necessarily detrimental to biodiversity conservation, unless they imply a large-scale decline in landscape heterogeneity. This is in agreement with the conclusions from previous studies on various species (e.g. Sergio et al. 2003, 2005; Marchesi et al. 2006). On the contrary, the declining availability of grassland could cause long-term biodiversity declines and should be urgently tackled through subsidies for extensive farming, aimed at halting the ongoing land abandonment. In conclusion, our data provide a first, coarse-level assessment of landscape-level gradients in vertebrate species richness. Because regional-levels of biodiversity set the upper limit attainable by local communities (e.g. Cornell and Lawton 1992), this study provides a large-scale framework for more detailed future studies. For example, amphibian richness is probably better modelled at the finer-scale pond-level, so as to incorporate the effect of variables such as pond isolation, internal characteristics of the pond (e.g. underwater vegetation, fish presence) and hospitality of the habitats surrounding the pond (e.g. Ray et al. 2002; Bosch et al. 2004). Similarly, many avian and reptile species may respond to environmental factors acting at a finer-grained scale than the one employed in our analyses.

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Determining high value areas for steppe birds in Spain: hot spots, complementarity and the efficiency of protected areas

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Abstract We have examined the distribution of 26 species of steppe birds in the Iberian Peninsula and the Balearic Islands within a grid of 5,070 10 × 10 km grid cells. The most valuable areas for steppe birds have been identified by selecting the upper 5% of the 10 × 10 km grid cells after a simple ranking based on the following criteria: species-richness, richness of rare species, rarity index, species vulnerability at Spanish, European and Global levels, and using an index combining the previous criteria. We have also used a heuristic algorithm to select those areas which offered most complementarity. The results have been analysed on a national scale and have been compared with those obtained by species assessments in previous status summaries. Finally, we have performed an analysis of the coverage afforded to locations which are valuable for steppe species by Natural Protected Areas (NPAs) and Special Protected Areas (SPAs), and an evaluation of the potential effects of temporal changes in species' threat-status.

The combined index was the most reliable criterion for defining hotspots, encompassing 15% of the species' distributions within 5% of the total area considered. This index showed a high level of geographical concordance with the other criteria (nearly 70% of the selected grid cells coincided). Analysis of complementarity delivered poorer results than simple rank-scoring. The analysis of the efficiency of NPA network showed a very low coverage (less than 2%) of the hotspots selected according to the Combined Index. Coverage of the SPA network was higher (nearly 45%), although it diminished (to <35%) when only steppe-defined SPAs were included. The geographical concordance between high-value areas selected using current status summaries and those chosen using earlier ones was low for European threat status (53.4%), intermediate (63.2%) for Spanish threat status and high for SPEC status (78.1%). The Combined Index showed a high level of geographical concordance between the old and new data (76.6%). We conclude that automatic

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scoring methods (identifying hotspots) are useful for selecting valuable areas and for analysing the efficiency of the network of protected natural spaces, as well as for examining the potential effects of status changes on hotspot definition. Furthermore, the Spanish SPA network does not cover the most important areas for steppe birds adequately.

Keywords Complementarity · Hotspots · Spain · Steppe birds · Threat-status changes · Efficiency of protected areas

Introduction

Recent years have seen the development of computational techniques for identifying high-value areas and establishing reserves, with the aims of optimising available resources, identifying the minimum extent of the areas needed to ensure protection and analysing the efficiency of the networks of protected spaces (Williams et al. 1996; Prendergast et al. 1993a, b; Lawton et al. 1994; Margules and Pressey 2000; Kati et al. 2004; Jiguet et al. 2005; Burgess et al. 2005). These procedures, based on simple rank-scoring on predefined criteria (sometimes termed hotspot estimation) or on applying algorithms (complementarity analysis), use basic, territory-based biological information, such as presence/absence of species (Williams et al. 1996; Rey Benayas and de la Montaña 2003) or the distribution of habitats or representative vegetational types (Kati et al. 2004), to identify zones having the highest scores under the criteria used (species-richness, number of rare or threatened species, landscape diversity, etc.). Irrespective of the technique used, automatic methods have been shown to be more efficient for designing networks of protected areas, in terms of the number of suitable sites and of total area selected, than those based on “expert” decisions (Pressey and Tully 1994; Pressey et al. 1997) or on the presence of key species as indicators of high diversity (Andelman and Fagan 2000), although they depend on the existence of basic territory data.

At present, one of the methods most employed to identify valuable areas is the identification of “hotspots”, not as was originally proposed by Myers (1988) and Myers et al. (2000), but as it has subsequently been applied more generally to areas with high species-diversity (Prendergast et al. 1993a, b; Lawton et al. 1994; Kerr 1997; Rey Benayas and de la Montaña 2003; Abellán et al. 2005; Sólymos and Fehér 2005), zones containing numerous rare species of restricted distribution (Williams et al. 1996; Kerr 1997; Rey Benayas and de la Montaña 2003; Abellán et al. 2005; Sólymos and Fehér 2005) and locations containing an abundance of threatened or vulnerable species (Faith and Walker 1996; Rey Benayas and de la Montaña 2003; Burgess et al. 2005). However, it has been noted on occasion that area-selection based on hotspots does not guarantee the inclusion of all the target species, especially when the number of species requiring protection is very large or when they can only be included by increasing the expanse of territory protected (Williams et al. 1996; Myers et al. 2000).

A heuristic algorithm has often been used to select the optimum number and extent of areas which will guarantee the inclusion of all the target species at the same time as minimising the amount of land needed to protect them (see Araújo and Williams 2001; Kelley et al. 2002; Kati et al. 2004; Sólymos and Fehér 2005 for recent examples). This procedure, termed complementarity analysis (Vane-Wright et al. 1991), has been found useful in the gap analysis of protected spaces (Scott et al. 1993;

Arponen et al. 2005) and in selecting areas where the territorial expanse required is very large and conflicts with more productive land-use interests must be minimised (Margules and Pressey 2000).

Steppe birds, those tied to open, treeless, agrarian landscapes (Suárez et al. 1997), are one of the most threatened avian communities in Europe, as shown in recent years by the marked population declines and range contractions which they have suffered (BirdLife International 2004; Santos and Suárez 2005; Burfield 2005). In Spain, where the steppe community is the most diverse and abundant in all Europe, such negative tendencies are associated with two processes (Madroño et al. 2004; Santos and Suárez 2005). On the one hand there is agricultural intensification, with consequent increases in fertiliser use, pesticide application and mechanisation. On the other, there is the abandonment of large areas of marginal land, which were formerly widely cultivated but are now experiencing an accelerated process of scrub encroachment (Suárez-Seoane et al. 2002). The particular characteristics of these species and their habitats demand that the expanses adequate for their conservation be very extensive, so having the potential for conflict with other land-users. There is thus a need to guarantee the selection of the best locations for incorporation into the protected spaces network, optimising the number and/or total extent of such areas.

The Birds Directive (Directive 79/409/CEE) obliges wild bird protection and their habitats in Europe and the establishment of a network of protected spaces to conserve them. It has led to the development of a series of Special Protection Areas (SPAs—ZEPAs in Spain) in all the member states of the European Union. SPAs in Spain were selected on specialist advice, given the scarcity of data on species distribution and abundance in Spain, required to apply computational techniques. The recent atlas of Spanish breeding birds (Martí and del Moral 2003) gives information on distributions on an intermediate scale (10×10 km quadrats) which allows the systematic application of criteria to identify important areas for bird conservation.

In this study we analyse the existing data on the distribution of breeding steppe birds in peninsular Spain and the Balearic Islands with three objectives: (i) to identify the most important areas (hotspots) for steppe birds by simple rank-scoring of richness, rarity and vulnerability criteria and of an index combining these hotspots, addressing questions such as how many steppe bird species are included in hotspots, what average percentage of their distribution is covered by them, or what is the geographical consistency among the criteria for hotspot definition, (ii) to compare these results with those after applying a heuristic algorithm to establish which are the minimum areas (complementarity areas) required to guarantee the conservation of all the breeding steppe species of the study area, and (iii) to compare the selected areas with the coverage of the existing networks of protected spaces, to assess their effectiveness. In addition, we attempt to analyse the effect which changes in the vulnerability-status of certain species may have on the selection of important areas.

Methods

Study area

The study area was the whole of peninsular Spain and the Balearic Islands (Fig. 1), a total of over $500,000$ km 2 . We used data on breeding bird presence within the Universal Transverse Mercator (UTM) grid of 10×10 km grid cells. Quadrats whose

Fig. 1 Map of Spain showing the main geographical and administrative regions mentioned in the present article



area was more than 50% within the sea or in extralimital countries were excluded, so that the final analysis was limited to 5,070 grid cells. Grid cell size was always 100 km² except for cells joining different UTM coordinate zones, and border cells.

Species

The 26 species included in the analysis (Appendix: Table 4) were selected in accordance with Suárez et al. (1997) on the basis of four associated criteria: (i) species typical of, or very frequent in, the Mediterranean region, (ii) ground-nesting species, (iii) species exclusive to treeless, principally flat zones, and (iv) species whose principal European population is in Spain. In addition, the list includes certain species which are not ground-nesters, such as the Lesser Kestrel (*Falco naumanni*), but which we consider to be clearly tied to steppe habitats by their preferential use of them (Bustamante 1997; Negro 1997). We have also included species such as the Skylark (*Alauda arvensis*), which are not strictly regarded as steppe species elsewhere but which may be unequivocally assigned to steppe ecosystems within the Iberian Peninsula (Suárez et al. 2003a). However, we have excluded those such as the Trumpeter Finch (*Bucanetes githagineus*) and Black Wheatear (*Oenanthe leucura*), which prefer semiarid habitats but are not steppe birds in the sense employed here in that they nest exclusively in rock cavities (see, for example, Snow and Perrins 1998).

The data used here are derived from the Spanish breeding bird atlas, the Atlas of Spanish Breeding Birds (Martí and del Moral 2003), which surveyed the whole of the Spanish state using 10 × 10 km grid cells. In total we have utilised 49,294 breeding records (species-in-grid-cell records) obtained for the 26 species in the 5,070 grid cells studied.

Criteria used

The following criteria were used to identify “Hotspot” grid cells and were applied successively to each grid cell: species-richness, richness of rare species, rarity index and species vulnerability at Spanish, European and Global levels. Species-richness

per grid cell was the number of species present in each, from zero up to a maximum of 26. Richness of rare species was based on the total of those species which were present in fewer than 50% of the grid cells in the study area, from zero up to a maximum of 19.

The “rarity” criterion has been used previously with reference to species of scarce distribution (Arponen et al. 2005; Sólymos and Fehér 2005; Rey Benayas and de la Montaña 2003; Abellán et al. 2005), arranged according to their frequency of occurrence in the original data. The high level of dispersion of the quadrats which were so assessed prompted the use of an *ad hoc* grouping of the species into three abundance classes, ranging from 0 (common species) to 10 (very rare species) (Appendix: Table 4). The rarity index per grid cell was then calculated as the sum of the abundance classes of the species present. Only rare or very rare species add values to the final score.

The vulnerability or threat criterion was based on the conservation status of each species, in terms of its abundance and distribution and the state of its populations. This criterion has been applied on three spatial levels, assessing the Spanish threat status (Madroño et al. 2004) whose categories are entirely based on those defined by the last IUCN Red List (IUCN 2001), European threat status (BirdLife International 2004) and European vulnerability with global concern, according to SPEC category (BirdLife International 2004). Each species was assigned a status value on a 0–10 scale (Appendix: Table 4) for each of the three spatial levels. The “vulnerability” value for each grid cell was calculated at each of the spatial levels by adding the scores for all the species present. Finally, all the information for each grid cell was expressed as a combined index by adding together all the values for each criterion, after standardisation of means.

Hotspot estimation

We have taken the highest scoring 5% ($n = 254$, including all cells which tied at the lowest score in this range) of the 5,070 10 × 10 km grid cells as a cut-off value for selecting the hotspots for each criterion. This percentage has been used in previous works (Prendergast et al. 1993a; Williams et al. 1996; Sólymos and Fehér 2005; Ramírez 2004) to represent the minimum area necessary to encompass the most important zones in a territory.

In addition, in order to evaluate variation in hotspot estimation resulting from changes in species’ status, an analysis of geographical concordance was carried out between the vulnerability criteria calculated from the recent status analyses (Madroño et al. 2004; BirdLife International 2004) and those based on earlier ones (Blanco and González 1992; Tucker and Heath 1994). The Combined Index was also recalculated on the basis of the latter criteria.

Complementary areas

We have applied a rarity/complementarity-based algorithm using ResNet software (Garson et al. 2002) to select the minimum number of grid cells which would guarantee the presence of the complete steppe bird community. This procedure emphasises the selection of areas which contain rare species and adds to these those additional areas which most complement them (the complementarity principle, Vane-Wright et al. 1991). The algorithm first selects the grid cell with the highest rarity value and

repeatedly adds those grid cells which most complement the selection until the objective of including the complete species-range is achieved (Kelley et al. 2002; Sarkar et al. 2002). The efficiency of this software has been tested against other similar algorithms (Kelley et al. 2002, after Margules et al. 1988) and it is complemented by algorithms which ensure that the selected areas are adjacent and contain a minimum of redundant information. See Garson et al. (2002) for more information on ResNet.

The algorithms used for calculating complementary areas are primed with a target, defined as a predetermined level of inclusion for each species. We have used three different targets (Appendix: Table 5): (i) the minimum number of grid cells needed to include 5% of the Spanish distribution of each species, (ii) the minimum number of grid cells needed to achieve as high a percentage of inclusion as possible for the less widely distributed species, and (iii) the minimum number of grid cells needed to obtain for each species the same percentage achieved in the Combined “Hot Spot” Index.

Protection efficiency assessment

The coverage afforded by the Natural Protected Areas (National, Natural and Regional Parks: NPAs) and the Special Protected Areas (SPAs) to the hotspots selected by applying the Combined Index was analysed, by simple intersection of maps using a GIS application (ArcGis 9.0 software, ESRI 2000). Provided that a sub-set of SPAs have been defined specifically by the presence of steppe birds, which has implications on how their habitats should be managed (the conservation of SPA-target species implies the conservation of their habitats, that is, steppe habitats in the present case), the protection efficiency of that particular SPA sub-set (steppe SPAs) was also examined. Those UTM grid cells more than 20% of whose area fell within NPAs ($n = 379$ grid cells) or SPAs ($n = 1,261$ grid cells) were previously selected.

Data analysis

The number of species present in each group of selected 10×10 km grid cells, and the occurrence of each species as a percentage of all the grid cells which it occupies in Spain, were calculated in all cases. The geographical concordance between grid cells selected according to the different criteria was analysed using a Spearman rank correlation test.

Results

Maxima and geographical pattern

None of the 5,070 grid cells analysed held the entire steppe bird community: the highest species-richness found per grid cell was 22 (mean \pm SD: 9.43 ± 4.25). The maximum was 15 species per grid cell if only rare species are considered (mean \pm SD: 4.39 ± 3.23).

Steppe bird species-richness was greatest in the Ebro valley, the northern and southern sub-mesetas (plateaus), the Extremaduran plains and the Guadalquivir valley (Fig. 2a). The principal mountain ranges and the northernmost parts of the Peninsula held least species. Only 35 grid cells (0.7% of the total) had no steppe

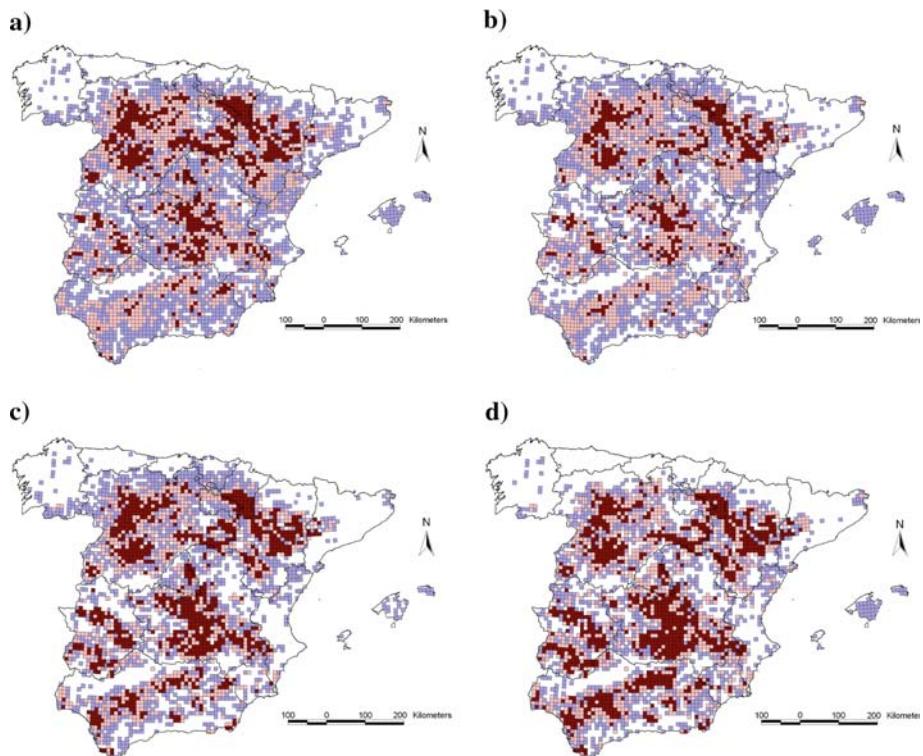


Fig. 2 Patterns of richness, rarity, threat, and combined index among 10×10 km grid cells in Spain: (a), total species richness; (b), rare species richness; (c), rarity; (d), Spanish Red Data Book status sensu Madroño et al. (2004); (e), European threat status sensu BirdLife International (2004); (f), SPEC category sensu BirdLife International (2004); (g), combined index; and (h), Combined Index hot spots selecting the 5% of all cells of highest ranking score. Maximum grid-cell scores are shown in brown. The remaining non-zero score classes are shown correspondingly pink (high scoring values), blue (median scoring values) and white (low and very low scoring values), so that maps can be compared irrespective of units of measure

species at all. A similar geographical pattern, with certain modifications, was apparent when the richness of rare species was analysed (Fig. 2b). Only 360 grid cells (7.1%) had no rare species. The distribution of rare species followed the pattern described above although it emphasised the importance of the Guadalquivir valley: including the Doñana area, and other parts of Andalucía, as well as parts of southern Extremadura (Fig. 2c). The map (Fig. 2d) obtained by applying the Spanish threat status criterion also highlights the same general areas, although it slightly minimises the importance of the Ebro valley, the uplands of the Sistema Ibérico and the northern sub-meseta, and the large expanses of cereal crops of the northern sub-meseta, but emphasises the southern sub-meseta, the Extremaduran plains and the Guadalquivir valley. Application of the European threat status and SPEC criteria again highlighted the importance of the Guadalquivir valley (Fig. 2e, f), within the same general distribution pattern described previously. The geographical consistency between the criteria used ($P < 0.0001$ for all the Spearman rank correlation tests between criteria) was repeated with the Combined Index, which included the Guadalquivir valley within the zones having high-value grid cells (Fig. 2g).

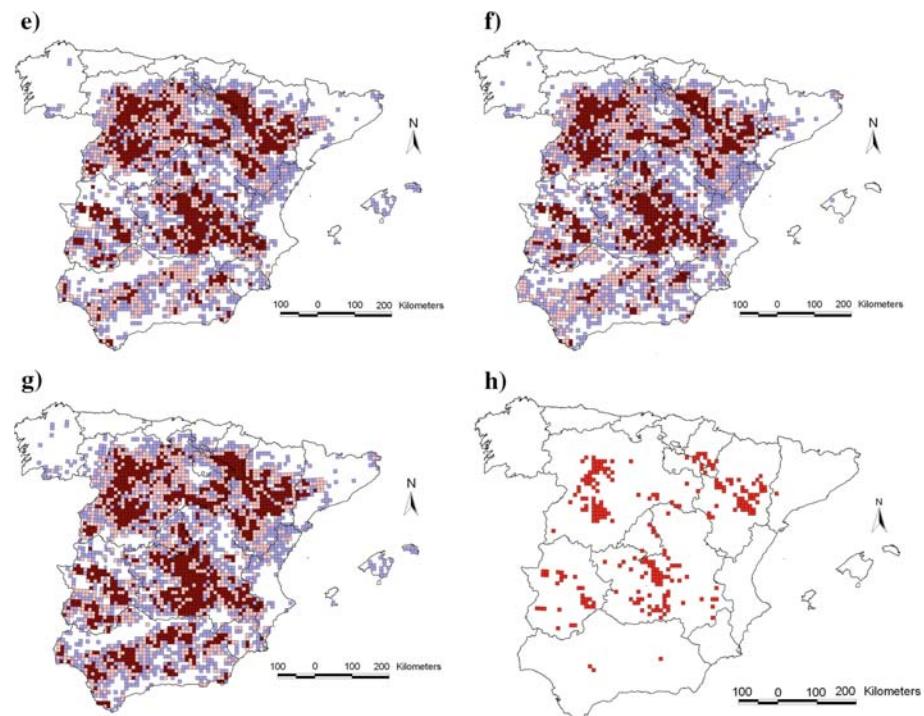


Fig. 2 continued

High-value areas for steppe birds in Spain

The hotspots we selected (the highest-scoring 5% of grid cells under each criterion) took in 25 out of the 26 species in all cases. Only the Cream-coloured Courser (*Cursorius cursor*) was always excluded from the selections, since it only breeds in one, not very species-rich, southern grid cell. The hotspots maps obtained via the different criteria assigned a mean of $174.8(\pm 17.6)$ grid cells per species. Each species was always assigned more than 25 grid cells, with the exception of the Collared Pratincole (*Glareola pratincola*) which was assigned only 23 grid cells in the species-richness hotspots map. In addition, the hotspots took in over 14% on average of the Spanish distributions of all the species, despite representing only 5% of the 5,070 analysed cells (Table 1). The Combined Index hotspots map (Fig. 2h) produced the best result, recording 25 species in 253 grid cells, representing 14.84% of the total Spanish distribution of all the species. The rare species richness hotspots map, based on only 19 species, achieved similar results to the other criteria (Table 1).

The species which were best represented by all the criteria were the most widely distributed ones, such as the Crested Lark (*Galerida cristata*) (255.86 ± 16.80 grid cells), Corn Bunting (*Miliaria calandra*) (255.29 ± 17.16 grid cells) or the Red-legged Partridge (*Alectoris rufa*) (255.14 ± 17.58 grid cells). The most poorly represented species were the Short-eared Owl (*Asio flammeus*) (30.14 ± 2.97 grid cells), Collared Pratincole (33.00 ± 8.76 grid cells) and Dupont's Lark (*Chersophilus duponti*) (55.29 ± 10.34 grid cells).

Table 1 Results of the different criteria used for selecting hotspots for steppe birds in Peninsular Spain and Balearic Islands, across 5,070 10 × 10 km UTM grid cells

| | SR | RSR | Rarity score | RDB 2004 | EU threat 2004 | SPEC index 2004 | Combined index | Complementary areas | Target 1 | Target 2 | Target 3 |
|------------------------------------------------|------------|-------------|--------------|------------|----------------|-----------------|----------------|---------------------|--------------|-------------|-----------|
| No. of grid cells chosen (n = 5,070) | 291 (5.7%) | 242 (4.77%) | 244 (4.8%) | 250 (4.9%) | 260 (5.1%) | 257 (5.1%) | 253 (5.0%) | 232 (4.58%) | 781 (15.40%) | 282 (5.56%) | |
| No. of species represented (n = 26) | 25 (96.2%) | 25 (96.2%) | 25 (96.2%) | 25 (96.2%) | 25 (96.2%) | 25 (96.2%) | 25 (96.2%) | 25 (96.2%) | 26 (100%) | 26 (100%) | 26 (100%) |
| Average percentage of distribution per species | 15.6% | 14.0% | 14.5% | 14.3% | 14.6% | 14.3% | 14.8% | 8.7% | 27.9% | 14.8% | |

SR, species richness; RSR, rare species richness, RDB 2004, status sensu Spanish Red Data Book (Madroño et al. 2004); EU-threat 2004 and SPEC, status sensu BirdLife International 2004

All the hotspot maps, and of course the Combined Index hotspot map (Fig. 2h), showed several typical geographical clusters (the other maps are available from the authors to anyone interested). These are: (a) the Ebro Valley, which has some of the most valuable grid cells, especially those located in its central range, (b) the Páramos (uplands) of the Sistema Ibérico, which hold hotspots in terms of species richness, richness of rare species and the Combined Index, (c) the Northern Meseta, with two different hotspot areas: the cereal plains in the north and the limestone uplands in the south, (d) the Southern Meseta, with three hotspot nuclei, one straddling its central range, another in the south, and the third in its east-southern extreme, and (e) Extremadura, with two discrete areas, La Serena in the south, and the Cáceres plains, although neither of these last figured within the species-richness and European threat status hotspot maps. Elsewhere, several isolated and dispersed cells were located outside these high-value nuclei, as in the Guadalquivir Valley or in the Madrid region.

The geographical concordance between hotspot maps estimated by the Spearman rank correlation was always significant (Table 2), although the average percentage of geographically concordant cells between the different indices was only 62.0% (Table 2). The highest mean concordance (around 69%) was between the Combined Index hotspots map and the others. Some concordance between criteria was low, as between Spanish threat status hotspots and species-richness hotspots (41.6%), and between diversity of rare species hotspots (47.8%) and European threat status hotspots (48.7%). On the other hand, the highest geographical concordance was between the rare species diversity and the combined index hotspots maps (83.0%). The 92 grid cells that were selected under all the criteria (high concordance cells) showed complete geographical concordance.

Complementarity

The areas selected by applying the complementarity algorithm always encompassed the 26 species studied but the resulting maps were less efficient than those obtained

Table 2 Spearman rank correlations and percentage of common cells among scores of criteria used for estimating Hot Spots for Spanish steppe birds, across 5,070, 10 × 10 km grid cells in Spain

| | SR | RSR | Rarity score | RDB 2004 | EU-threat 2004 | SPEC 2004 | Combined index 2004 |
|---------------------|-------|-------|--------------|----------|----------------|-----------|---------------------|
| SR | 1 | | | | | | |
| | 100 | | | | | | |
| RSR | 0.792 | 1 | | | | | |
| | 66.56 | 100 | | | | | |
| Rarity score | 0.693 | 0.844 | 1 | | | | |
| | 54.62 | 74.19 | 100 | | | | |
| RDB 2004 | 0.567 | 0.628 | 0.770 | 1 | | | |
| | 41.62 | 47.75 | 64.12 | 100 | | | |
| EU-threat 2004 | 0.712 | 0.762 | 0.775 | 0.637 | 1 | | |
| | 56.98 | 62.99 | 64.71 | 48.69 | 100 | | |
| SPEC-2004 | 0.728 | 0.728 | 0.797 | 0.682 | 0.782 | 1 | |
| | 58.84 | 58.92 | 67.56 | 53.64 | 65.71 | 100 | |
| Combined index 2004 | 0.732 | 0.826 | 0.903 | 0.790 | 0.770 | 0.820 | 1 |
| | 59.24 | 71.53 | 83.03 | 66.78 | 64.10 | 70.81 | 100 |

All correlations were significant ($P < 0.05$). SR, species richness; RSR, rare species richness; RDB 2004, status sensu Spanish Red Data Book (Madroño et al. 2004); EU-threat 2004 and SPEC, status sensu BirdLife International 2004)

by the simple rank-scoring methodology. As its first target the algorithm selected 232 grid cells (4.6% of the total), although these were widely dispersed across the entire study area except within the Ebro valley (Fig. 3a). In addition, it under-represented some other areas which were highlighted in the hotspots analysis, such as the plains of Extremadura and the southern sub-meseta. The second target selected 781 grid cells (15.4% of the total), significantly more than the intended 5% coverage of the Iberian peninsula, although the areas chosen corresponded well to the best possible distribution of high value areas for steppe birds (Fig. 3b). The third target needed 296 grid cells in order to include 100% of the species, 29 grid cells more than those selected using the Combined Index hotspots map. The application of this third target gave rise to differences from the regions selected by simple rank-scoring since it did not include grid cells in the uplands of the Sistema Ibérico, although it did incorporate zones in the Guadalquivir valley (Fig. 3c).

Changes in species-status

Changes in species-status according to successive national status statements in Spanish Red Data Books (Blanco and González 1992; Madroño et al. 2004) and

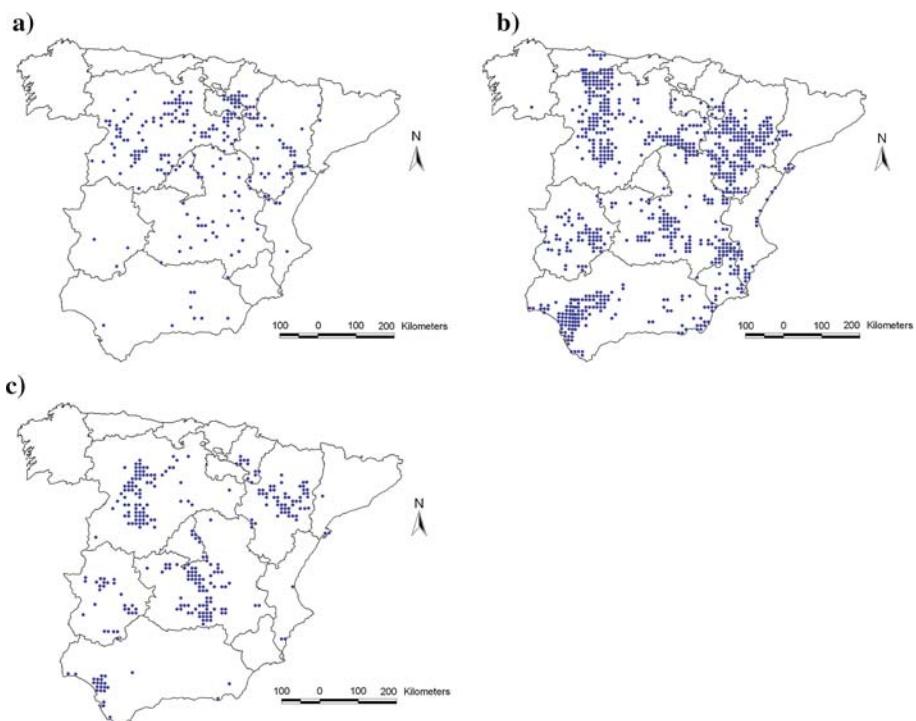


Fig. 3 Results of the complementarity analysis used to select the minimum number of grid cells guaranteeing the presence of the complete steppe bird community based on three different targets: (a) target 1, minimum number of grid cells needed to include 5% of the Spanish distribution of each species; (b) target 2, minimum number of grid cells needed to achieve the highest possible percentage of inclusion for the less widely distributed species; and (c) target 3, minimum number of grid cells needed to obtain for each species the same percentage achieved in the Combined Index hotspot map

European ones (Tucker and Heath 1994; BirdLife International 2004) brought about significant changes in the high-value areas selected by simple rank-scoring. Hence, the overall geographical concordance between statements was low for European threat status (53.4%), intermediate (63.2%) for Spanish threat status and high for SPEC status (78.1%), showing which status appraisals had revealed the most important changes in species-status. The Combined Index, using as it does a larger number of criteria, showed a high level of geographical concordance between the old and new data (76.6%).

Protection efficiency assessment

The NPA network encompassed 25 of the 26 steppe bird species, although seven of them, apart from the Cream-coloured Courser which was not included, appeared in fewer than 25 grid cells (0.5% of the 5,070 10 × 10 km grid cells) within NPAs (Table 3): Short-eared Owl, Lesser Short-toed Lark (*Calandrella rufescens*), Dupont's Lark, Collared Pratincole, Great Bustard (*Otis tarda*), Pin-tailed Sandgrouse (*Pterocles alchata*) and Black-bellied Sandgrouse (*Pterocles orientalis*). Only 5 (2.0%) of the 253 grid cells selected in the Combined Index hotspots map fell within the NPA network.

The coverage of steppe birds by the SPAs was better. Again excluding the Cream-coloured Courser, the remaining species were all included in more than 30 grid cells within the SPA network (Table 3), which also covered nearly 24% of the Spanish distribution of these species. A total of 113 grid cells (44.7%) of the 253 selected by Combined Index hotspots map were included within the SPA network.

The results altered when only those SPAs defined specifically by the presence of steppe birds (steppe-SPAs) were included. Three species: Short-eared Owl, Lesser Short-toed Lark and Collared Pratincole appeared in fewer than 25 grid cells in steppe-SPAs. The steppe-SPAs included 8.2% on average of the Spanish distribution of the steppe bird species and only 84 (33.0%) of the grid cells included in the Combined Index map were included within the steppe-SPA network. Similarly, only 27 (29.35%) of the 92 high concordance grid cells were in the network. When high concordance grid cells were added to the SPAs and steppe-SPAs networks the Spanish distribution of the species covered by the networks improved, especially for the case of steppe-SPAs (26.4 and 12.1%, respectively).

Discussion

The high-value areas for steppe birds in peninsular Spain identified by simple rank-scoring techniques (hotspot location) are geographically cohesive, supported by expert opinion and correspond with the appropriate biogeographical conditions. They also show a good match with those regions which have been traditionally defined as “steppe” or “pseudosteppe” in Spain (Suárez et al. 1992, 1997; Santos and Suárez 2005). Algorithm-based methods have been found to be less efficient in defining these zones, given that they have selected marginal zones or have indicated the same geographical pattern as the scoring methods but at the cost of including larger areas. Finally, the effectiveness of the networks of protected spaces for protecting high-value steppe bird areas has been shown to be either very low (NPAs) or moderate (SPAs), failing to cover numerous very important sites.

Table 3 Representation (no. of grid cells and percentage) of each species inside NPAs, SPAs, and within steppe SPAs only, and re-evaluation after including high concordance cells (HCC)

| Species | NPAs | | SPAs | | Steppe SPAs | | SPAs + HCC | | Steppe SPAs + HCC | |
|-------------------------------------------------------------|--------------|------|----------------|-------|----------------|-------|----------------|-------|-------------------|-------|
| | No. of cells | | No. of cells % | | No. of cells % | | No. of cells % | | No. of cells % | |
| | No. | % | No. | % | No. | % | No. | % | No. | % |
| <i>Circus cyaneus</i> Hen Harrier | 33 | 4.71 | 200 | 28.57 | 53 | 7.57 | 219 | 31.29 | 72 | 10.29 |
| <i>Circus pygargus</i> Montagu's Harrier | 50 | 2.31 | 403 | 18.59 | 139 | 6.41 | 456 | 21.03 | 204 | 9.41 |
| <i>Falco naumanni</i> Lesser Kestrel | 36 | 3.51 | 238 | 23.17 | 101 | 9.83 | 287 | 27.95 | 162 | 15.77 |
| <i>Alectoris rufa</i> Red-legged Partridge | 274 | 5.90 | 1,104 | 23.77 | 170 | 3.66 | 1,159 | 24.96 | 237 | 5.10 |
| <i>Colinus cristatus</i> Quail | 169 | 4.58 | 808 | 21.92 | 155 | 4.21 | 860 | 23.33 | 218 | 5.91 |
| <i>Tetrax tetrax</i> Little Bustard | 20 | 1.55 | 264 | 20.50 | 132 | 10.25 | 318 | 24.69 | 197 | 15.30 |
| <i>Otis tarda</i> Great Bustard | 5 | 0.95 | 166 | 31.50 | 111 | 21.06 | 203 | 38.52 | 159 | 30.17 |
| <i>Burhinus oedicnemus</i> Stone Curlew | 53 | 2.43 | 419 | 19.22 | 145 | 6.65 | 473 | 21.70 | 211 | 9.68 |
| <i>Cursorius cursor</i> Cream-coloured Courser ^a | 0 | 0.00 | 0 | 0.00 | 0 | 0.00 | 0 | 0.00 | 0 | 0.00 |
| <i>Glareola pratincola</i> Collared Pratincole | 13 | 6.81 | 38 | 19.90 | 5 | 2.62 | 48 | 25.13 | 23 | 12.04 |
| <i>Pterocles orientalis</i> Black-bellied Sandgrouse | 13 | 1.55 | 140 | 16.73 | 117 | 13.98 | 239 | 28.55 | 176 | 21.03 |
| <i>Pterocles alchata</i> Pin-tailed Sandgrouse | 12 | 2.75 | 108 | 24.71 | 64 | 14.65 | 151 | 34.55 | 118 | 27.00 |
| <i>Asio flammeus</i> Short-eared Owl | 1 | 1.37 | 29 | 39.73 | 17 | 23.29 | 37 | 50.68 | 27 | 36.99 |
| <i>Alauda arvensis</i> Skylark | 127 | 4.51 | 684 | 24.30 | 130 | 4.62 | 733 | 26.04 | 188 | 6.68 |
| <i>Chersophilus duponti</i> Dupont's Lark | 5 | 2.16 | 60 | 25.97 | 34 | 14.72 | 71 | 30.74 | 46 | 19.91 |
| <i>Galerida cristata</i> Crested Lark | 167 | 4.31 | 817 | 21.08 | 163 | 4.21 | 872 | 22.50 | 230 | 5.93 |
| <i>Galerida theklae</i> Thekla Lark | 197 | 6.74 | 726 | 24.82 | 112 | 3.83 | 772 | 26.39 | 167 | 5.71 |
| <i>Melanocorypha calandra</i> Calandra Lark | 56 | 2.69 | 398 | 19.11 | 146 | 7.01 | 452 | 21.70 | 212 | 10.18 |
| <i>Calandrella brachydactyla</i> Short-toed Lark | 68 | 3.20 | 443 | 20.83 | 138 | 6.49 | 496 | 23.32 | 203 | 9.54 |
| <i>Calandrella rufescens</i> Lesser Short-toed Lark | 19 | 7.82 | 58 | 23.87 | 22 | 9.05 | 77 | 31.69 | 42 | 17.28 |
| <i>Anthus campestris</i> Tawny Pipit | 97 | 4.85 | 539 | 26.94 | 104 | 5.20 | 586 | 29.29 | 157 | 7.85 |
| <i>Oenanthe oenanthe</i> Northern Wheatear | 127 | 5.45 | 665 | 28.52 | 123 | 5.27 | 710 | 30.45 | 178 | 7.63 |
| <i>Oenanthe hispanica</i> Black-eared Wheatear | 172 | 5.87 | 647 | 22.08 | 103 | 3.52 | 697 | 23.79 | 164 | 5.60 |
| <i>Cisticola juncidis</i> Fan-tailed Warbler | 104 | 4.39 | 422 | 17.81 | 109 | 4.60 | 471 | 19.88 | 166 | 7.01 |
| <i>Sylvia conspicillata</i> Spectacled Warbler | 70 | 5.50 | 287 | 22.55 | 65 | 5.11 | 319 | 25.06 | 100 | 7.86 |
| <i>Miliaria calandra</i> Corn Bunting | 235 | 5.23 | 1,001 | 22.29 | 169 | 3.76 | 1,056 | 23.51 | 236 | 5.25 |

^a Only breeds in one peninsular grid cell

High-value areas for steppe birds in Spain

The results show that peninsular Spain is very species-rich, at least for the group of steppe species considered by this study. Although none of the grid cells included the entire steppe community (the maximum was 22 out of 26 species), only 35 grid cells held none of them. The high average number of steppe species present per grid cell (9.4 ± 4.3) is explicable, in part, by the excellent conditions for steppe birds offered by a large part of Spanish territory, with great expanses devoted to cereal crops together with extensive zones of natural shrub-steppe (including esparto *Stipa tenacissima* formations) and semiarid pastures (Santos and Suárez 2005). In addition, the high mean diversity values per grid cell suggest that, at least on the scale considered, the various species have a marked tendency to occur together, despite apparent differences in habitat selection (Santos and Suárez 2005; Morales et al. 2006), which is probably due to the mosaic nature of the steppe landscapes, where patches of crops, fallows, uncultivated land and pasture alternate.

The frequent presence in northern Spain and indeed in mountain areas of more typically central-European species such as the Skylark and Hen Harrier (*Circus cyaneus*) increases the species-richness of zones which have not traditionally been regarded as steppes, as does the wide distribution of such species as the Crested Lark, Thekla Lark (*Galerida theklae*), Corn Bunting and Red-legged Partridge. The status of Spain as a crucial country for steppe birds is consolidated by the high frequency of rare species (4.4 ± 3.2 species/grid cell), which were absent from only 360 grid cells (7.1%).

The selected hotspots drew in with precision both the steppe bird community of the study area (25 out of 26 species), and its distribution, given that just 5% of the area considered encompassed over 14% of the grid cells where steppe birds occurred. The sole species excluded, the Cream-coloured Courser, was only known to breed for certain in one grid cell.

The high geographical concordance between criteria, something which has also been observed in other analyses on a similar scale (Prendergast 1993a; Kerr 1997), allowed the consistent detection of the most valuable regions for steppe birds in the Iberian peninsula and showed that these coincide with zones traditionally defined as “steppe” or “pseudosteppe” in Spain (for a biogeographic revision, see Santos and Suárez 2005). These, in ascending order of importance are: the plains of Extremadura, the cereal croplands of the Northern and Southern Mesetas, the open plateaus of the Sistema Ibérico, and, especially, the Ebro valley. The clumping of key sites around a few nuclei was especially notable in view of the scarcity of peripheral high-value grid cells, which may indicate a loss of habitat quality, particularly in the south of the peninsula, where agricultural intensification has been proportionately greater. A possible consequence of this is the gradual disappearance of marginal areas, which could generate an element of negative feedback as conservation efforts may become concentrated on current high-value areas.

Despite the high spatial concordance between criteria, a more detailed examination reveals differences between them, which may determine the selection of high-value areas and the allocation of conservation funds, as a function of the criterion used. Some authors have previously indicated that it may be best to apply multiple criteria together, in order to avoid such geographical discrepancies (Hoctor et al. 2000; Kati et al. 2004, see however Sólymos and Fehér 2005). Indeed the Combined Index showed the highest concordance with the other criteria: around 69% of

geographic concordance. Thus, it was deemed a good synthetic indicator of high-value areas. The rare species diversity hotspots criterion, considering only 19 species, achieved similar results to the Combined Index and so could also serve as the sole criterion. A more conservative approach could make use of the high concordance grid cells (very hotspots), those which were selected under all the criteria.

Complementarity

The results of the complementary areas analysis proved to be sub-optimal or poorer than those obtained by the more parsimonious simple-rank scoring method (hotspot identification). Applying a heuristic algorithm does not guarantee the best possible solution but rather the achievement of the proposed targets (completeness in surrogate coverage), the efficient selection of the smallest area possible (Kelley et al. 2002). Neither does it guarantee that rejected sites are less deserving of conservation than the selected ones, given that the selection process is “blind” and determined solely by the rules of the algorithm (Pressey et al. 1997).

In the present case, the high dispersion of the grid cells obtained under target 1 did not correspond with what expert opinion (and hotspot maps) indicated to be the most valuable areas. This result corresponds with those indicated by other authors, who have indicated the propensity of heuristic algorithm methods to select areas located at the extremes of distributions (Williams et al. 1996; Araújo and Williams 2001; Kati et al. 2004; Sólymos and Fehér 2005), although the high level of dispersion of the selected grid cells reduces bias arising from the concentration of high-value zones in just a few areas. Target 2 produced equally inefficient results, given that it selected a significantly larger area than that obtained by identifying hotspots. With target 3, the need to incorporate 100% of the species led to including 29 grid cells more than those defined using the Combined Index (see Kati et al. 2004; Kelley et al. 2002), and resulted in the under-representation of significant steppe bird zones, such as the uplands of the Sistema Ibérico, where there are some of the most important concentrations of threatened species such as Dupont’s Lark.

Changes resulting from variation in species status

Analyses based on old and new data on species vulnerability gave rise to notable changes in the mapping of important areas, leading to a low level of geographical concordance between superseded and current status summaries. The low geographical concordance between the European threat status map obtained after Tucker and Heath (1994) and the one obtained after BirdLife International (2004) was due to the significant status changes shown by numerous species during the intervening period, such as the Great Bustard, Northern Wheater (*Oenanthe oenanthe*) and the Corn Bunting (which show increasing threat status) and the Collared Pratincole, Pin-tailed Sandgrouse, or the Short-eared Owl (which show decreasing threat status). The analysis of Global Concern threat status (SPEC) gave less variation between the two data sources considered, given that only the Little Bustard (*Tetrax tetrax*), Northern Wheater and Corn Bunting increased in threat status notably, so that the two sets of SPEC maps show greater geographical concordance. Regarding Spanish threat status, the differences are explicable in that the first data source indicated few species, with none recorded in over 1,600 grid cells, compared with only 180 grid cells in the latter summary. The intervening period has seen the inclusion in

the threatened-in-Spain list or an improvement in status of many steppe species, such as the Little Bustard, Stone Curlew, Dupont's Lark, the Black-eared Wheatear, the Cream-coloured Courser, the Short-toed Lark (*Calandrella brachydactyla*) and the Lesser Short-toed Lark.

Selection of high-value sites, be it by identifying hotspots or by analyses of complementarity, is useful for designated protected areas and, consequently, may be relevant to fund allocation and to change conservation policies. This being so, the choice of criteria for selecting areas requires the greatest caution, given that status changes of a few species may result in significant differences in determining high-value areas, as occurred in the case of the region of Catalonia, where the geographical concordance between the two data sets was nil. This is especially relevant in countries like Spain, where the conservation policies are full transferred to the regional governments. The use of Combined Indices may moderate such undesirable outcomes (Williams et al. 1996). In addition to its use in the identification of protected areas, the analysis of changes in vulnerability status can be understood as a dynamic tool to redirect conservation strategies and funds.

Protection efficiency assessment

The efficiency of the NPA network has been shown to be clearly inadequate: although the protected spaces sheltered 25 out of the 26 steppe bird species, the representation of high-value areas was marginal, at fewer than 2% of the grid cells selected by the Combined Index. The analysis of the SPA network gave better results, particularly since most species were well represented (in over 30 grid cells) and because nearly 45% of the hotspots indicated by the Combined Index were included in SPAs. Nevertheless, most SPAs have not been established on account of the presence of steppe birds. This could partly explain the under-representation of several species (Short-eared Owl, Lesser Short-toed and Dupont's Larks, Collared Pratincole, Great Bustard, and the two sandgrouses) within the SPA network. The steppe-SPA sub-group, despite having significantly higher values under the Combined Index than other grid cells, was still poorly effective since it included barely 33% of the most valuable 10 × 10 km grid cells in Spain according to that index, and only 29% of the high concordance grid cells. The protection efficiency would significantly improve if these high concordance grid cells were protected, especially in the case of the steppe-SPAs networks (from 8.2 to 12.1% on average of the Spanish distribution of the steppe bird species).

The effectiveness of a network of protected spaces depends on the degree of coverage offered to its target species, those which motivated the sites' establishment. So far, no NPAs have been declared on account of steppe birds, with perhaps the exception of the Villafáfila Regional Park, in the cereal croplands of the northern sub-meseta. In this respect, it is important to realize that, given the high level of overlap between SPAs and NPAs, the protection of steppe species and habitats heavily relies on the SPA network, which has two important conservation consequences. First, in Spain, the level of legal protection is much lower in SPAs than in NPAs (for example, the only restriction to actions such as infrastructure building and urbanization SPAs may come through the environmental impact assessment procedure—see Suárez et al. 2003b—while in NPAs are usually limited by the corresponding Management Plans). Second, only the small proportion of each species' distribution included in steppe-SPAs will be managed

in a “steppe-specific” manner. This is despite steppe species being the bird community which has shown the severest decline both within Europe as a whole (BirdLife International 2004) and in Spain (Santos and Suárez 2005), and despite the great extent of steppe and pseudo steppe habitats in Spain (Suárez et al. 1992).

The low to moderate efficiency of the network of steppe-SPAs can only be explained by the absence of defined methods and explicit criteria for the designation of areas for bird protection. Such areas have frequently been designated on account of flagship species, such as the Great Bustard, with the result that many vulnerable or species-rich areas have remained outside the network. The establishment of protected space networks on the basis of the presence of flagship or umbrella species has been found to be poorly effective before (Kerr 1997; Andelman and Fagan 2000). It is also possible that within Spain priority in SPA designation has been given to other bird groups, such as forest communities, for which the effectiveness of protection has been shown to be appreciably superior (Ramírez 2004). In any event, it must be borne in mind that just because a grid cell does not form part of the top 5% does not mean that it lacks conservation value.

Finally, the current analysis is extremely conservative, given that the presence of a species in a grid cell overlapped by an SPA does not necessarily mean that the species was present within the SPA itself. The coincidence of species and protected areas also does not guarantee the existence of specific protection measures, something which is especially evident in Spain where the steppe zones find themselves threatened by the processes of agricultural intensification, land abandonment, urbanisation and fragmentation by large-scale infrastructure, among others. In this context, the efficiency results regarding steppe-SPAs are particularly meaningful, as they show how some of the more widely extended, but more rapidly transformed habitats in Spain, are poorly covered by the SPA network, which has clear implications for the conservation of steppe-bird communities.

Conclusions on the usefulness of the methodology

Since the Natura 2000 network of protected spaces was definitively established, the EU member states have been obliged to evaluate its success periodically. Steppe birds are one of the most threatened groups on a European scale, which makes them a primary objective for conservation measures. The use of automatic techniques allows the relatively easy and rapid evaluation of the success of the SPA network and other conservation policies or actions, in addition to detecting new zones for incorporation or where conservation measures should be maximised. To this end, scoring methods used to define hotspots could be more effective than using heuristic algorithms, whose character is more indicative than prescriptive (Pressey et al. 1997). In any event, the efficacy of the methods resides in the quality of the data used (Kati et al. 2004), whose collection and processing must be given priority.

Appendix

Table 4 Species list, number of 10×10 km grid cells occupied in Spain (Canaries Island not included), and scores assigned for each species and criteria

| | No of cells | Rarity score ^a | RDB 04 score ^b | 2004 EU threat score ^c | 2004 SPEC score ^d |
|------------------------------------------------------|-------------|---------------------------|---------------------------|-----------------------------------|------------------------------|
| <i>Circus cyaneus</i> Hen Harrier | 700 | 10 | 0 | 2 | 5 |
| <i>Circus pigargus</i> Montagu's Harrier | 2,168 | 5 | 7 | 0 | 1 |
| <i>Falco naumanni</i> Lesser Kestrel | 1,027 | 10 | 7 | 2 | 10 |
| <i>Alectoris rufa</i> Red-legged Partridge | 4,644 | 0 | 1 | 5 | 7 |
| <i>Coturnis coturnix</i> Quail | 3,686 | 0 | 1 | 2 | 5 |
| <i>Tetrax tetrax</i> Little Bustard | 1,288 | 10 | 7 | 7 | 10 |
| <i>Otis tarda</i> Great Bustard | 527 | 10 | 7 | 7 | 10 |
| <i>Burhinus oedicnemus</i> Stone Curlew | 2,180 | 5 | 5 | 7 | 5 |
| <i>Cursorius cursor</i> Cream-coloured Courser | 1 | 10 | 10 | 10 | 5 |
| <i>Glareola pratincola</i> Collared Pratincole | 191 | 10 | 7 | 5 | 5 |
| <i>Pterocles orientalis</i> Black-bellied Sandgrouse | 837 | 10 | 7 | 5 | 5 |
| <i>Pterocles alchata</i> Pin-Tailed Sandgrouse | 437 | 10 | 7 | 5 | 5 |
| <i>Assio flammeus</i> Short-eared Owl | 73 | 10 | 5 | 2 | 5 |
| <i>Alauda arvensis</i> Skylark | 2,815 | 0 | 0 | 2 | 5 |
| <i>Chersophilus duponti</i> Dupont's Lark | 231 | 10 | 10 | 2 | 5 |
| <i>Galerida cristata</i> Crested Lark | 3,876 | 0 | 0 | 2 | 5 |
| <i>Galerida theklae</i> Thekla Lark | 2,925 | 0 | 0 | 2 | 5 |
| <i>Melanocorypha calandra</i> Calandra Lark | 2,083 | 5 | 0 | 5 | 5 |
| <i>Calandrella brachydactyla</i> Short-toed Lark | 2,127 | 5 | 7 | 5 | 5 |
| <i>Calandrella rufescens</i> Lesser Short-toed Lark | 243 | 10 | 5 | 5 | 5 |
| <i>Anthus campestris</i> Tawny Pipit | 2,001 | 5 | 0 | 5 | 5 |
| <i>Oenanthe oenanthe</i> Northern Wheater | 2,332 | 5 | 0 | 5 | 5 |
| <i>Oenanthe hispanica</i> Black-eared Wheater | 2,930 | 0 | 5 | 2 | 7 |
| <i>Cisticola juncidis</i> Zitting Cisticola | 2,369 | 5 | 0 | 0 | 0 |
| <i>Sylvia conspicillata</i> Spectacled Warbler | 1,273 | 5 | 3 | 0 | 0 |
| <i>Miliaria calandra</i> Corn Bunting | 4,491 | 0 | 0 | 5 | 7 |

^a Rarity score: Assigned thus: 0, species whose frequency of occurrence in the totality of grid cells considered was >50%, 5, species whose frequency of occurrence was 25–50%, and 10, species whose frequency of occurrence was <25%

^b Vulnerability in Spain: Scores assigned according to the classifications in the Red Data Book 2004 (IUCN 2001; Madroño et al. 2004): 0 = not evaluated, 1 = data deficient, 3 = least concern, 5 = near threatened, 7 = vulnerable, and 10 = endangered and critically endangered species

^c European Vulnerability, sensu European Threat Status 2004 (BirdLife International 2004): 0 = secure, 1 = localised, 2 = depleted, 3 = rare, 5 = declining, 7 = vulnerable, and 10 = endangered and critically endangered species

^d European Vulnerability with global Concern, assigned according to SPEC category in 2004 (BirdLife International 2004): As SPEC 1994 (Tucker and Heath 1994), but SPEC 4 is now Non SPEC Europe, with value = 1

Table 5 Criteria (percentage of the distribution of each species in peninsular Spain) used in the definition of targets for calculating complementary areas by ResNet

| Species | Criterion 1 | Criterion 2 | Criterion 3 |
|-------------------------------------------------------------|-------------|-------------|-------------|
| <i>Circus cyaneus</i> Hen Harrier | 5 | 25 | 10 |
| <i>Circus pygargus</i> Montagu's Harrier | 5 | 5 | 11 |
| <i>Falco naumanni</i> Lesser Kestrel | 5 | 10 | 19 |
| <i>Alectoris rufa</i> Red-legged Partridge | 5 | 5 | 5 |
| <i>Coturnix coturnix</i> Quail | 5 | 5 | 7 |
| <i>Tetrax tetrax</i> Little Bustard | 5 | 10 | 19 |
| <i>Otis tarda</i> Great Bustard | 5 | 25 | 33 |
| <i>Burhinus oedicnemus</i> Stone Curlew | 5 | 5 | 11 |
| <i>Cursorius cursor</i> Cream-coloured Courser ^a | 100 | 100 | 0 |
| <i>Glareola pratincola</i> Collared Pratincole | 5 | 100 | 19 |
| <i>Pterocles orientalis</i> Black-bellied Sandgrouse | 5 | 25 | 27 |
| <i>Pterocles alchata</i> Pin-tailed Sandgrouse | 5 | 50 | 38 |
| <i>Asio flammeus</i> Short-eared Owl | 5 | 100 | 45 |
| <i>Alauda arvensis</i> Skylark | 5 | 5 | 7 |
| <i>Chersophilus duponti</i> Dupont's Lark | 5 | 100 | 26 |
| <i>Galerida cristata</i> Crested Lark | 5 | 5 | 7 |
| <i>Galerida theklae</i> Thekla Lark | 5 | 5 | 6 |
| <i>Melanocorypha calandra</i> Calandra Lark | 5 | 5 | 12 |
| <i>Calandrella brachydactyla</i> Short-toed Lark | 5 | 5 | 11 |
| <i>Calandrella rufescens</i> Lesser Short-toed Lark | 5 | 100 | 26 |
| <i>Anthus campestris</i> Tawny Pipit | 5 | 5 | 9 |
| <i>Oenanthe oenanthe</i> Northern Wheatear | 5 | 5 | 8 |
| <i>Oenanthe hispanica</i> Black-eared Wheatear | 5 | 5 | 7 |
| <i>Cisticola juncidis</i> Fan-tailed Warbler | 5 | 5 | 8 |
| <i>Sylvia conspicillata</i> Spectacled Warbler | 5 | 10 | 9 |
| <i>Miliaria calandra</i> Corn Bunting | 5 | 5 | 6 |

Criterion 1: 5% of each species' distribution. Criterion 2: 5% for species in more than 2,000 grid cells, 10% for species in 1,000–2,000 grid cells, 25% for species in 500–1,000 grid cells, 50% for species in 250–500 grid cells, and 100% for species in less than 250 grid cells. Criterion 3: Same as distribution achieved by the Combined Index hotspot map

^aOnly breeds in one grid cell

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The Berger–Parker index as an effective tool for monitoring the biodiversity of disturbed soils: a case study on Mediterranean oribatid (Acari: Oribatida) assemblages

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Abstract Recent data on oribatid mites (Acari: Oribatida) indicates that Mediterranean soil communities tend to show uneven patterns of species abundance distribution (SAD) that are well fitted by a simple model such as the geometric series. In the case of linear distributions, the fraction of total sampled individuals that is contributed by the most abundant species, known as the Berger–Parker index, synthetically describes the SAD of disturbed communities. This study assessed the bioindicator potential of the Berger–Parker index by comparing its variations among Mediterranean oribatid assemblages under different types of soil disturbance. The index significantly changes between undisturbed and disturbed soils reaching the highest values in areas with strong physical disturbance due to agricultural management. The Berger–Parker index is therefore a practical and effective tool for monitoring biodiversity impairment linked to human disturbance in soil ecosystems.

Keywords Berger–Parker index · Diversity · Oribatid mites · Soil · Disturbance

Introduction

Soil microarthropods play an important role in nutrient cycling by comminution of litter and grazing: the former increases the surface area for microbial attack, while the latter stimulates microbial growth (Seastedt 1984; Visser 1985).

Microarthropods can also act on soil structure and humus formation through their mechanical activity, faecal pellet deposition and release of nutrients (Wallwork 1983; Norton 1985). The preservation of their biodiversity and the characterization of the

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main factors affecting community patterns are therefore of crucial importance for the management and conservation of soil (Noti et al. 2003; Lindo and Visser 2004; Caruso and Migliorini 2006a); however, community studies are challenging for researchers because they require great taxonomical skill and expertise (Migliorini et al. 2002; Caruso and Migliorini 2006a).

Among microarthropods, oribatid mites (Acari, Oribatida) have been proposed as bioindicators of soil quality (van Straalen 1998; Behan-Pelletier 1999; Prinzing et al. 2002; Maraun et al. 2003; Lindo and Visser 2004), but their complex taxonomy limits practical applications (Caruso and Migliorini 2006a). There is therefore a need to identify easy-to-calculate, synthetic descriptors able to discriminate disturbed soil ecosystems from undisturbed ones.

According to previous studies (Usher 1985; Hågvar 1994; Chung et al. 2000; Caruso and Migliorini 2006b), the species abundance distribution (SAD) of oribatids from disturbed ecosystems follows a very uneven pattern (a large number of low density species and few high density species), which can be modelled by the geometric series. Caruso and Migliorini (2006b) recently reformulated the geometric series, and the present paper aimed at showing the link between the new formulation of this model and the Berger–Parker index (Berger and Parker 1970; Magurran 1988). Recent data on oribatids indicate that this index, which accounts for the dominance of the most abundant species over the summed abundance of all species in the assemblage, is significantly affected by environmental conditions (Noti et al. 2003) and by anthropogenic disturbance such as metal pollution and clear-cut harvesting (Fountain and Hopkin 2001; Lindo and Visser 2004).

In the present study we produced new data and re-analysed our own literature data (Migliorini et al. 2002; Migliorini et al. 2005; Caruso and Migliorini 2006a) in order to compare oribatid mite assemblages from Mediterranean soil ecosystems affected by different types of disturbance. The aim of the study was to evaluate whether the Berger–Parker index can represent a simple but effective tool for a community approach to environmental monitoring of soil ecosystems.

Materials and methods

The Berger–Parker index and the geometric series

The reformulation of the geometric series by Caruso and Migliorini (2006b) is summarised by the following equations:

$$N_i = r^{i-1} \quad (1)$$

$$K = \frac{N_S}{N_T} \quad (2)$$

$$K \cong \frac{r - 1}{r} \quad (3)$$

$$S = \frac{\log N_S}{\log r} + 1 \quad (4)$$

where N_i is the abundance of the i -th species, N_S indicates the abundance of the most abundant species, N_T and S respectively are the total number of individuals and of species in a community sample, and K and r are the two correlated parameters of the

model. The non-zero constant r is the common ratio of the geometric series. Indeed, it is the ratio between one term and the preceding one. Thus, if species are ranked from the least abundant ($i = 1$) to the most abundant ($i = S$) and the obtained abundance distribution is governed by a geometric series, the ratio between the abundance of one species and the preceding one is constant. The reformulation by Caruso and Migliorini (2006b) outlines the relationships between the geometric constant r and the ratio K of equation (2), which therefore synthesises the community SAD. Furthermore, K is equivalent to the Berger–Parker dominance index (Berger and Parker 1970; Magurran 1988). As the geometric distribution is usually observed in disturbed communities (Usher 1985; Hågvar 1994; Chung et al. 2000; Caruso and Migliorini 2006b), we hypothesised that the Berger–Parker index can discriminate between disturbed and undisturbed oribatid assemblages.

Study areas

Seven study areas were selected in grassland and agricultural environments of southern Tuscany (central Italy, Table 1) where soil arthropod assemblages usually show moderate or strongly uneven distribution patterns (Migliorini et al. 2002; Migliorini et al. 2003). Four areas were disturbed by human activity: (1) a mine dump area where soil is contaminated by Zn, Cu and Pb (average of 7000, 2500 and 2000 µg/g d.w. respectively) (2) a shooting range where pellets pollute the soil with an average Pb concentration of 1000 µg/g d.w. (3) an agricultural area for intensive production of corn (4) a managed sainfoin (*Onobrychis sativa*) grassland for pasture. A fifth, naturally disturbed area was located in a grassland affected by floods (about one moderate flood each year).

Two undisturbed areas were located in two nature reserves: (1) a grassland dominated by *Bromus erectus* with a thin organic layer (2) the so-called Biancana badlands consisting of Pliocene clay domes no higher than 200 m. The southern slopes of these domes lack vegetation, while the northern slopes are covered by scarce herbaceous or rare shrub vegetation (*Spartium junceum*, *Crataegus monogyna*).

Data collection and standardization

All data on agricultural and flooded areas are new, whereas part of the data from the other areas was reported in previous publications (Migliorini et al. 2002; Migliorini et al. 2005; Caruso and Migliorini 2006a). Although all data derive from studies that aim to describe the effects of different types of disturbance on oribatid fauna and were obtained in the same laboratory, preliminary data standardization and sorting

Table 1 Study areas

| Locality | Geographical coordinates | Type of disturbance |
|-------------------|--------------------------|-----------------------------------------------------|
| Pietraporciana | 43°00' N; 11°48' E | Undisturbed (nature reserve) |
| Lucciolabella | 43°02' N; 11°44' E | Undisturbed (nature reserve) |
| La Foce | 43°00' N; 11°33' E | Natural (weak floods) |
| Clay Pigeon | 43°18' N; 11°26' E | Chemical (metal pollution) |
| Forni dell'Accesa | 42°58' N; 10°54' E | Chemical (metal pollution) |
| Leonina | 43°17' N; 11°27' E | Physical and chemical (agriculture, corn field) |
| Montaperti | 43°19' N; 11°07' E | Physical and chemical (agriculture, sainfoin field) |

was necessary (Underwood 1997; Clarke and Warwick 1994; McCune and Mefford 1999). Sampling units ranged from $5 \times 5 \times 7$ cm to $20 \times 20 \times 5$ cm in the different studies. Community multivariate analysis was thus performed on standardized data to enable comparison among areas (Clarke and Warwick 1994; McCune and Mefford 1999). Only adults were classified (to the species level) and counted (for details on sampling and laboratory procedures see: Migliorini et al. 2002; Migliorini et al. 2003; Migliorini et al. 2005, Caruso and Migliorini 2006a).

In theory the different sampling size does not bias the comparison of the Berger–Parker index among study areas, since the index is a dimensionless number. Moreover, the sampling size does not affect SAD patterns within the range of commonly adopted units: depending on the characteristics of the study area, the same sampling unit can display uneven as well as even species abundance patterns (Usher 1985; Hågvar 1994) and this is probably due to the high sample density of these animals (Caruso and Migliorini 2006b). Equation (2) was thus used to calculate the Berger–Parker index for each replicate sample with no further standardization.

The dominance pattern of oribatids can show temporal variability in relation to annual life cycles (Noti et al. 2003). Unfortunately, the strategy for temporal replication of sampling differed among study areas. Indeed, sampling plots within the two undisturbed areas were sampled monthly from December 1999 to January 1999 (five replicates for each sampling date). The flooded grassland as well as the crop field and the managed sainfoin field were sampled in June 2004 and June 2005 (six replicates from each area). Metal-polluted areas were sampled only in October 2001 and January 2003 (six replicates from the most metal-polluted plots). Due to this heterogeneity, a preliminary one-way ANOVA was performed at $P < 0.05$ to verify that the Berger–Parker index did not differ significantly within each area at the different sampling dates, thus enabling spatial comparison between areas. In all areas the Berger–Parker index did not significantly vary among sampling dates (ANOVA P -level always > 0.5), thus indicating temporal stability over a one year period, at least in the studied areas.

Data analysis

After the preliminary temporal analysis based on the whole set of replicates (150 samples), six replicates were randomly selected from each area, and a one-way ANOVA was performed to test the null-hypothesis that the Berger–Parker index does not significantly vary among areas. This procedure allowed the compilation of a balanced dataset (equal number of randomly selected observations) for spatial comparison among areas. Before running ANOVA, data were tested ($P < 0.05$) for normality and homogeneity of variance, and the post-hoc Tukey test was used to determine the significance of differences among areas (Underwood 1997).

Permutational Multivariate Analysis of Variance (PERMANOVA; McArdle and Anderson 2001; Anderson 2005) was used to test the null-hypothesis that oribatid assemblages do not differ among the seven areas. This test is an analogue of the Multivariate Analysis of Variance (MANOVA) but can also deal with non-normal, discontinuous or aggregated data. PERMANOVA relies on a permutation procedure to obtain the P -values and thus, according to Anderson (2005), no parametric assumptions are required to determine species distribution. The PERMANOVA test has been shown to be suitable for testing multivariate hypotheses on terrestrial communities (Fulé et al. 2005; Hilszczański et al. 2005). As in the case of one-way

ANOVA, the test was based on six replicates randomly selected from each study area (for a total of 42 analysed replicates). The percentage frequencies of species were determined to interpret the PERMANOVA output.

Statistical analyses were performed using the STATISTICA 5 (StatSoft Inc., Tusla, USA) package along with the FORTRAN program by Anderson (2005).

Results

The mean Berger–Parker index values increased from undisturbed to disturbed areas (Fig. 1). One-way ANOVA detected significant differences among the seven areas ($F_{6, 41} = 6.52, P < 0.001$). The post-hoc Tukey test indicated that the sainfoin field differed significantly from all areas except the corn field, and that the corn field differed significantly from undisturbed areas but not from alluvial and metal-polluted areas.

The PERMANOVA test revealed that assemblages differed significantly ($F_{6, 41} = 6.93, P < 0.001$) among study areas, and the t-pairwise *a posteriori* PERMANOVA test indicated that differences were significant ($P < 0.01$) between paired areas.

Significant differences obtained by PERMANOVA are due to large differences in species composition and abundance. The mean (\pm S.D.) percentage of species shared by areas was $18 \pm 5\%$, indicating a high degree of difference in species composition (high beta-diversity). Based on a total of 93 species, 53% were present only in one area, while 18, 12, 4.5, 9 and 3.5% were respectively present in two, three, four, five or six areas.

The most frequent species (arbitrarily defined as those present in at least five areas) were *Tectocephalus sarekensis*, *T. velatus*, *Epilohmannia cylindrica*,

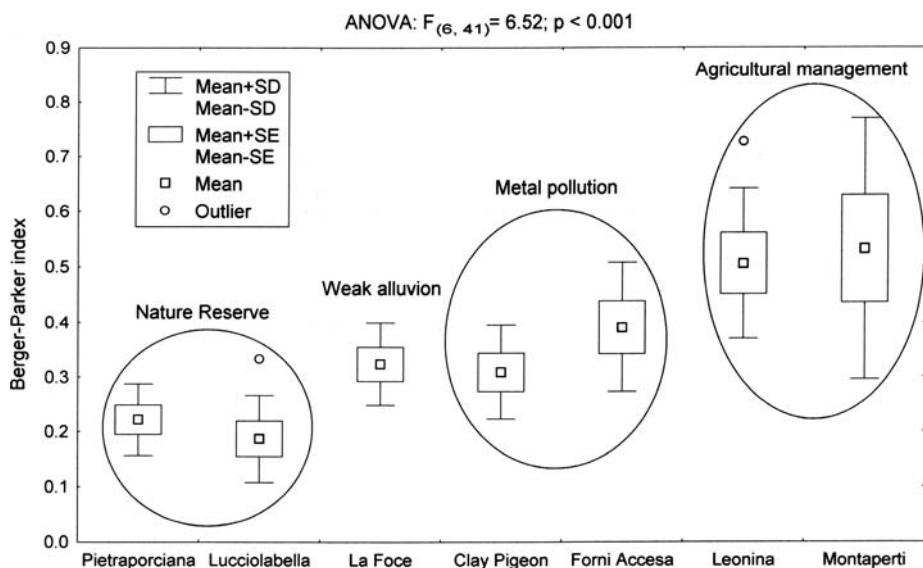


Fig. 1 Berger–Parker index (mean, S.D., S.E., $n = 6$) in the seven study areas

Punctoribates punctum, Scheloribates pallidulus, Peloptulus phaeonotus, Sphaerochthonius splendidus, Peloptulus phaeonotus, Ramusella gyrate, Allogalumna alamellae, Micropia minus, Suctobelbella sp. and Ceratozetes laticuspidatus, but the relative contribution of these species to the total number of oribatids differed among areas. For instance, in the sainfoin field *P. punctum* accounted (mean \pm S.D.) for $59 \pm 22\%$ of individuals, but in the other six areas the mean percentage ranged from zero (two areas) to 25% (corn field). Similar patterns were found for each of the most frequent species, with species such as *S. splendidus* dominating undisturbed areas and others such as *T. sarekensis* dominating disturbed areas.

Discussion

The main hypothesis of this paper was confirmed by data on oribatid assemblages from Mediterranean areas with different types of disturbance. The mean fraction of total sampled individuals that is contributed by the most abundant species (Berger–Parker index) changes from undisturbed to disturbed soils and differences are highly significant when the intensity of disturbance is high, as in the case of agricultural management involving physical and structural transformation of the soil environment (Maraun et al. 2003; Ponge et al. 2003). This pattern is coherent with the observation that disturbed communities are characterised by highly uneven distributions, which can be described by simple models such as the geometric series (Usher 1985; Hågvar 1994; Chung et al. 2000). In species assemblages characterised by this abundance distribution a few dominant species account for most of the total number of individuals (Magurann 1988; Caruso and Migliorini 2006b); such assemblages are therefore characterised by high Berger–Parker index values.

Calculation of the Berger–Parker index requires the collection of data on the total number of individuals and on the densest species; the latter generally belong to widespread, well-known taxa (Migliorini et al. 2005) and can thus be easily identified by non-expert environmental technicians after a brief period of training. In particular, the method is easy to apply to disturbed or naturally stressed communities that are species-poor and in which a few species account for a large part of the total number of individuals (May 1975; Usher 1985; Hågvar 1994).

The biological meaning of the Berger–Parker index has not yet been accurately assessed (Magurann 1988), but some hypotheses can be formulated on the basis of available evidence and models (Hubbell 2001; Chase 2005; Hubbell 2005, McGill et al. 2006). Under disturbance, oribatid communities share similar dominance patterns and are dominated by widely distributed, opportunistic species such as *Tectocephalus sarekensis*, *T. velatus*, *Scheloribates pallidulus*, *Punctoribates punctum* (Franchini and Rockett 1996; Behan-Pelletier 1999; Migliorini et al. 2004; Caruso and Migliorini 2006b). However, the results of this study as well as data from other Mediterranean areas (Migliorini et al. 2002; Migliorini et al. 2004) indicate high β -diversity at different scales (from local to regional), because a few widely distributed species dominate stressed soils but the identity of these species changes within areas and among areas that are characterised by different faunal contexts.

Disturbance can decrease the density of sensitive species and lead to their extinction, thereby allowing colonisation by opportunistic species; however, the process, which determines the identity of the successful species, remains unknown (Caruso and Migliorini 2006b). It is interesting to note that the patterns of

dominance (Berger–Parker index and geometric series) and β -diversity (species composition) described for disturbed soils have also been observed in naturally stressed and fragmented ecosystems (Caruso et al. 2005). According to the neutral model of Hubbell (2001), this similarity could be explained by: (1) the randomness of colonisation (2) the filter effect of habitat fragmentation (3) the rate of colonisation; According to Hubbell's neutral theory, high colonisation rates shift distributions towards even patterns (i.e., low Berger–Parker index values), increasing migration fluxes between meta and local communities so that species compositions become similar. In this process, the identity of species is of minor importance: a high α -diversity in the meta-community (source species pool) and high fragmentation among local-communities (species sink) determines high β -diversity among local communities and uneven patterns (high Berger–Parker index values), as well as low α -diversity at a local scale (Hubbell, 2001).

However, human-caused disturbance often leads to the extinction of sensitive species, thus making disturbed systems more susceptible to the colonisation of opportunistic species (Chase 2005). The environmental and ecological features of the system after disturbance may therefore simply but significantly determine the identity of the opportunistic and colonising species (Behan-Pelletier 1999; Chase 2005). Through niche selection processes, the new environmental features may be responsible for the extinction of the original species and the positive selection of a subset of species from the whole set of potentially colonising species (Caruso and Migliorini 2006b). Successful colonising species will dominate the assemblage, determining an increase in the Berger–Parker index, which corresponds to well-documented successional processes (Scheu and Schulz, 1996; Zaitsev et al. 2006).

Unfortunately, the lack of knowledge on the auto-ecology and biology of oribatids makes it difficult to definitely solve this issue, and the possible interaction between neutral and niche selection processes cannot be excluded (Chase 2005; McGill et al. 2006). For instance, although much progress has recently been made on the feeding ecology of oribatid mites (Schneider et al. 2004; Schneider and Maraun 2005), no general patterns have emerged. Different experiments on different species have yielded contrasting results: choice experiments on the selection of fungi reveal limited trophic differentiation (Schneider and Maraun 2005), but analyses based on stable isotope ratios ($^{15}\text{N}/^{14}\text{N}$) indicate different trophic niches among different species (Schneider et al. 2004). These studies mainly suggest that some oribatid species are highly specialized while others are more generalist, and that a single oribatid species may consist of different specialized populations. In the latter case, the species as a taxon could be interpreted as a generalist but, at a local scale, the population belonging to this species may actually be highly specialized (Schneider et al. 2004).

In conclusion, this study shows that the Berger–Parker index is an effective, simple tool for environmental monitoring of soil ecosystems. Further research on soil biodiversity should aim to: (1) improve the collection of data on α -diversity, β -diversity and species dominance patterns (2) improve basic biological research on poorly known taxa such as mites, in order to understand the impact of community change and human disturbance on the ecosystem. Specifically, there is the need to develop experimental studies able to assess responses of mite species to specific levels of different environmental stresses. This knowledge will allow a correct interpretation of soil biodiversity patterns in the context of ecosystem management and conservation.

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The effects of fire on communities, guilds and species of breeding birds in burnt and control pinewoods in central Italy

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Abstract Breeding bird communities in burnt and unburnt residual pinewoods were studied over 3 years by line-transect method, following a catastrophic fire event in Castelfusano (Rome, Central Italy; July 2000). We applied bootstrap procedures to evaluate whether the observed data were true or just produced by chance, and then examined the emerging patterns at three levels: community, guild and species levels. At the community level, fire acted on breeding bird communities by altering especially the total abundance patterns: the species abundance decreased in the burnt pinewood compared to the residual one, but other parameters were not significantly affected by fire. As a consequence of fire, the destruction and structural simplification of the canopy and shrubby component, as well as the increase of edge habitat and patchiness at landscape scale, induced a turnover in species between pinewoods. Species turnover was higher at the burnt than at the residual pinewoods, during all the 3 years of study. At the guild level, the forest species decreased strongly in terms of richness and abundance in the burnt pinewoods, contrary to the edge and open habitat species which increased in terms of richness, abundance and evenness. Edge species showed the highest turnover in burnt pinewood during the whole period of study. At species level, after an a priori subdivision (based on bibliographic search) of the various species in two ecological guilds (forest versus edge species), it was found that an a posteriori statistical analysis confirmed the expected trend, i.e. that the species which decreased significantly in burnt pinewood were essentially the forest species, whereas the species which increased were essentially the edge/open habitat ones. Overall, in order to investigate the effects of

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fire catastrophes on birds, the guild approach seems more exhaustive than the taxonomic community approach, where intrinsic confounding trends are present.

Keywords Breeding birds · Community ecology · Fire · Mediterranean · Pinewoods · Forest species · Edge species · Diversity · Species richness · Abundance · Evenness

Introduction

Anthropogenic or natural fire acts by means of both direct and indirect effects on the biocenotic and structural components of the ecosystems (e.g. Braun-Blanquet 1926; Kulmholtz-Lordat 1938; Ahlgren 1974; Prodon et al. 1987; Trabaund 1989). In several ecosystems, including the Mediterranean evergreen chaparral (=macchia), fire is a natural regulator of the phytocenosis structure, as it occurs regularly during the dry summer (e.g. Marchand 1990; Pantis and Mardiris 1992). However, the effects of fire on a particular ecosystem will depend on their frequency, intensity and season (Gill 1975; Lemckert et al. 2003). Studies on the fire effects on the natural communities of organisms were traditionally carried out in order to understand their consequences at the ecosystem level (Braun-Blanquet 1926; Kulmholtz-Lordat 1938), but recent studies have highlighted the role of fires even at the population, community and landscape levels (e.g. Naveh 1975; Prodon et al. 1987; Trabaund 1989; Herrando et al. 2003; Pitzalis et al. 2005; Pinto et al. 2006; Rugiero and Luiselli 2006).

In the Mediterranean forest bird communities, fire may determine a landscape heterogeneity which increases the species richness, thus favouring the colonization of edge species linked to ecotonal habitats. Consequently, a dynamic species turnover with substitution of those species which are specialists of the inner forest with other species which are generalist or synanthropic could be observed (Bendell 1974; Herrando et al. 2003).

Changes of the habitat structure can in turn influence the composition of the breeding bird communities (MacArthur and MacArthur 1961; Cody 1968; Wiens 1969; James 1971; Anderson and Shugart 1974; Conner et al. 1975; Whitmore 1977; Herrando and Brotons 2002; Herrando et al. 2003; Moreira et al. 2003; Brotons et al. 2005). Some studies have shown, in particular, a similarity among bird communities in burnt and cut pinewoods (Blake 1982). Taylor and Barmore (1980) have observed that a destructive fire or a heavy cut of the vegetation produce similar effects on breeding bird communities. Moreover, following fire or clear-cutting there may be the induction of a changement of the trophic structure of the community (Hagar 1960; Bock and Lynch 1970; Michael and Thornburg 1971; Kilgore 1971; Webb et al. 1975; Taylor and Barmore 1980).

In the Mediterranean area, data on fire disturbance effect on breeding bird communities and guilds are still scarce (e.g. Farina 1980; Meschini 1980; Protti 2001; Ukmar et al. 2004).

Aim of this study was to analyse, during 3 years, the effects of fire-induced habitat changes on the structure of the breeding bird communities in a Mediterranean ecosystem. Data are discussed in terms of the relative influence of fire at three hierachic community-scale levels: assemblages (herein named ‘communities’ for simplicity), guilds and species.

Materials and methods

Study area

The Castelfusano area ($41^{\circ} 44'N$; $12^{\circ} 19'E$), characterised by a forest mosaic landscape, is a part of the “Litorale romano” State Reserve (16,200 ha) positioned on the southwestern side of the metropolitan area of Rome (Central Italy). This area has an environmental continuity with the “Presidential Estate of Castelporziano” (Scarascia Mugnozza 2001). Contrary to Castelporziano, where an abundant coverage of sclerophyllous Mediterranean vegetation is present, in our study area this vegetation type has been largely replaced since the 17th century with pinewoods (prevalently, *Pinus pinea*), and only residual fragments of Mediterranean vegetation (both maquis and oak forest) are present. The bioclimate is Mediterranean (Blasi 1994). Soil is primarily sandy-pebbles and two main ecosystem units are related respectively to dunal and interdunal depression systems (Arnoldus 1981). The first unit is characterised by prevalence of artificial pinewoods and of *Quercus ilex* woods (*Viburno-Quercetum ilicis* vegetation), and Mediterranean bushland (prevailing: *Phillyreo-Arbutetum* vegetation). The second unit is characterised by the prevalence of hygrophilous mixed wood of *Populus alba* and/or *Quercus robur* (*Fraxino-quercetoroboris* and *Populeto albae* vegetations).

On July 2, 2000 a large fire stroke the Castelfusano pinewood in the inner side of the forest devastating about 400 ha and affecting primarily two vegetation types (see Bologna 2002): (1) the mature *Pinus pinea* wood, about 100-year-old, with patchiness cover and underbrush constituted mainly of *Quercus ilex* and local presence of other Mediterranean plant species; and (2) the recent *Pinus pinea* wood, about 50-year-old, with patches of Mediterranean bush.

In the mature pinewood, fire destroyed the canopy layer as well as the underbrush and the Mediterranean shrub. Following the fire, a wood cut was done in the burnt pinewood for eliminating the residual vegetation and to predispose the area to reforestation (Pitzalis et al. 2005).

The study area, inside the mature pinewood, was 312 ha wide and can be divided in two habitats:

(a) *Residual pinewood* (Rp): an old-growth pinewood (*Pinus pinea*) with underbrush constituted of *Quercus ilex* and, occasionally, *Quercus robur* in the humid areas. This pinewood has been marginally affected by fire, and it has been damaged only at the underbrush level. In our study, this habitat type was considered as the control to be compared with the burnt pinewood (=treatment).

(b) *Burnt pinewood* (Bp): in this area the fire destroyed completely the underbrush, and the few trees surviving the devastation were those of *Pinus pinea* and *Quercus ilex*.

The structural characterization of the vegetation for both Rp and Bp has been sorted using the Range Finder Circle Method (James and Shugart 1970, modified) performing four plots of 0.04 ha for each habitat type (dbh: 1.40 m).

No substantial differences emerged in the tree-size distribution between the two habitat types. The difference in the total density of the larger trunks (i.e. with a diameter > 38 cm) in the two habitat types was not statistically significant (Yates' corrected χ^2 test = 0.55, $df = 1$, $P = \text{NS}$; Fig. 1).

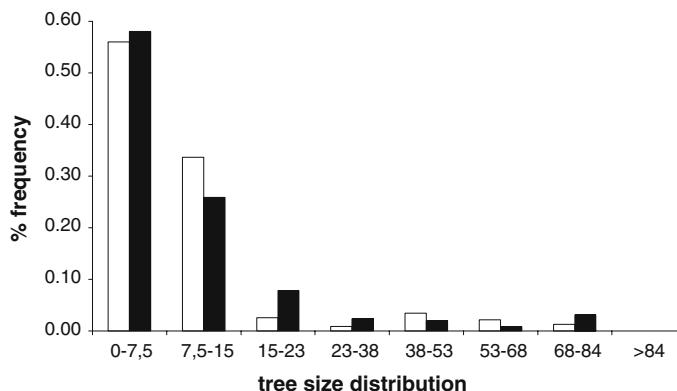


Fig. 1 Tree-size distribution (=relative frequency of the trunks divided by diameter classes in each studied habitat type; diameter in cm) at the study area. White: Bp; N = 255; black: Rp; N = 232). For more details, see “Methods”

Due to its extension, intensity, duration and consequences at the ecosystem level, the fire event affecting the study area could be certainly defined as a catastrophic rather than a disturbance event (see Hobbs and Huenneke 1992; Farina 2001).

Protocol

In each of the two habitat types we defined a line-transect. The line-transect method was used to study the bird community structure (Merikallio 1946; Järvinen and Väistönen 1976; see Telleria and Garza 1983, for Mediterranean ecosystems). We applied the transect method for small habitat patches according to Villard et al. (1995) rather than other alternative methods (e.g. mapping method, points count, etc.) because it is preferable in spatially constrained areas. Indeed, the mapping method (see Bibby and Burgess 1992) is excessively time consuming at a heterogeneous landscape scale whereas the point counts method (see Blondel 1975) is more indicated for homogenous large-scale habitats and hence it does not allow the acquisition of a valuable dataset (i.e. number of points) in small sized patches.

Each transect, 700 m long and 25 m wide (i.e. approximately 22% of the whole study area), was walked with constant speed ($1.5 \text{ km} \times \text{h}^{-1}$) in the early hours of the morning (7.00–11.00 a.m.), in both Bp and Rp. We recorded all the bird individuals (i) seen or (ii) heard in voice or in song within 25 m at right and at left of the observer. Data recorded from both methods were pooled in the analyses.

We conducted two transects/month from April to June 2001, 2002 and 2003 in each habitat type (36 transects and 1080 min of sampling effort). Bird records in community studies are always underestimated (Bibby and Burgess 1992); consequently for each month (and for each surveyed vegetation type) we considered the maximum values/month. For each breeding bird species, median values of abundance among the three values obtained for each yearly study period (April–June) were retained for the analysis.

We walked the line-transects in morning time (see above); consequently, species with crepuscular or nocturnal activity, such as the Strigiformes, were not considered. Also individuals of species that flew up the canopy, and that relate to a spatial scale

wider than that of the habitat type (e.g. species with high vagility, such as the Falconiformes), were not considered.

Species in the communities were clustered a priori in two ecological groups (guilds; see Verner 1984), according to their presumed linkage with forest (*forest sensu lato* species) or edge/open habitat preferences (edge species; Table 1). Data on the ecological preference of the various species were gathered from the peer-reviewed literature (e.g. Moore and Hooper 1975; Cieslak 1985; Opdam et al. 1985; Møller 1987; Hinsley et al. 1995; Bellamy et al. 1996).

Statistical procedures

We calculated the following community/guild parameters:

- Species richness (S) and, at guild level, forest *s.l.* (Sf) and edge (Se) species richness;
- Relative frequency as proportion of the individual forest *s.l.* (Fr_f) and edge (Fr_e) species on the total;
- Shannon total diversity index (H) with $H = -\sum fr \ln(fr)$; with fr = frequency of each species (Shannon and Weaver 1963); forest *s.l.* (H_f) and edge (H_e) diversity index;
- Simpson dominance index ($C = \Sigma fr^2$; Simpson 1949);
- Evenness index (J); where $J = H/H_{\max}$ (Lloyd and Ghelardi 1964) and $H_{\max} = \ln S$ (Pielou 1966); forest *s.l.* (J_f) and edge (J_e) evenness index;
- total abundance of the overall (TOTAB), forest *s.l.* (AB_f) and edge (AB_e) species for each breeding season in both habitats (Rp and Bp), expressed as individuals/km.

A β_T -turnover index (Wilson and Shmida 1984; see Ricotta 2002, for an application) was calculated between 1st and 3rd year of study:

$$\beta_T = [g(S) + l(S)]/2\alpha_m$$

where $g(S)$ is the number of species gained (i.e. newly recorded), and $l(S)$ is the number of species lost between 2001 and 2003; α_m corresponds to the average species richness among 1st and 3rd year of study (where species richness is a measure of α -diversity *sensu* Whittaker 1960).

A species richness/evenness diagram was carried out to evaluate the structural difference between communities in a Cartesian space (see Battisti et al. 1997).

Table 1 List of the breeding bird species found at the study area, and their relative attribution to the forest *sensu lato* versus edge/open habitat types

| Habitat | Species |
|-----------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Forest | <i>Streptopelia turtur</i> , <i>Cuculus canorus</i> , <i>Upupa epops</i> , <i>Jynx torquilla</i> , <i>Picus viridis</i> , <i>Dendrocopos major</i> , <i>Picoides minor</i> , <i>Troglodytes troglodytes</i> , <i>Erithacus rubecula</i> , <i>Luscinia megarhynchos</i> , <i>Turdus merula</i> , <i>Sylvia atricapilla</i> , <i>Phylloscopus collybita</i> , <i>Regulus ignicapillus</i> , <i>Muscicapa striata</i> , <i>Aegithalos caudatus</i> , <i>Parus caeruleus</i> , <i>Parus major</i> , <i>Sitta europaea</i> , <i>Certhia brachydactyla</i> , <i>Oriolus oriolus</i> , <i>Garrulus glandarius</i> , <i>Sturnus vulgaris</i> , <i>Fringilla coelebs</i> |
| Edge and open habitat | <i>Streptopelia decaocto</i> , <i>Galerida cristata</i> , <i>Motacilla alba</i> , <i>Cisticola juncidis</i> , <i>Sylvia cantillans</i> , <i>Sylvia melanocephala</i> , <i>Passer italiae</i> , <i>Serinus serinus</i> , <i>Carduelis carduelis</i> , <i>Carduelis chloris</i> , <i>Emberiza cirlus</i> |

To test whether the bird community parameters at the burnt and at the residual plots were structured as indicated by the application of the above-mentioned formulas, or whether the data distribution was dependent merely on chance effects, we applied a bootstrapping procedure to the actual data matrix. Bootstrapping is a method for estimating the sampling distribution of an estimator by resampling with replacement from the original sample (Gotelli and Graves 1996). It is distinguished from the jackknife procedure, used to detect outliers and cross-validation, whose purpose is to make sure that results are repeatable. We contrasted the actual data matrix with data generated by 5000 random bootstraps, and then applied a matrix permutation test, the Mantel's test (Manly 1997). The pertinent statistic is

$$\Sigma_{(i < j)} a_{ij} \times b_{ij}$$

which gives an indication of the correlation between the true matrices (a) and (b). In fact, if each distance matrix were vectorised, this is the equivalent of an uncentered covariance between the vectors. If the two distances are small in the same places, and big in the same places the statistic will be large indicating a strong link between the distances. In order to actually test the significance of such a link, a permutation test is performed: the null distribution is obtained by permuting the elements of a to obtain what is denoted by Πa , keeping the matrix symmetric, and recomputing the statistic as follows:

$$\Sigma_{(i < j)} \Pi a_{ij} \times b_{ij}$$

What is useful here is the idea of a vectorial covariance between distance matrices, which we will apply to the special case of correlation matrices which are in fact similarities. The vector covariance between two matrices was defined as their natural inner product:

$$\text{Cov}V(A, B) = \text{Tr}(B'A)$$

and their vectorial correlation as:

$$RV(A, B) = \text{Cov}V(A, B) / \sqrt{\text{Cov}V(A, A) \text{Cov}V(B, B)} = \text{Tr}(A'B) / \sqrt{\text{Tr}(A'A) \text{Tr}(B'B)}$$

Bootstrap tests sample from a distribution satisfying our null hypothesis of no difference between our true data matrices and data matrices randomly generated.

All tests, two-tailed and with alpha set at 5% if not otherwise explicitly indicated, were performed by the software SPSS 11.5 for Windows, apart from Monte Carlo permutations, which were performed by the softwares 'EstimateS 7.50' and 'Ecosym 700'.

Results

Community level

Thirty-five species of birds were observed: 30 in residual pinewood (Rp; range: 26–29) and 30 in burnt pinewood (Bp; range: 16–28; Table 2). As for Rp, after 5,000

Table 2 Year-by-year values of the structural parameters of the bird communities at the study area

| | 2001 | 2002 | 2003 |
|----------|--------|--------|--------|
| Rp | | | |
| <i>S</i> | 28 | 29 | 26 |
| <i>H</i> | 2.83 | 2.85 | 2.67 |
| <i>C</i> | 0.092 | 0.098 | 0.121 |
| <i>J</i> | 0.851 | 0.846 | 0.819 |
| TOTAB | 225.75 | 244.31 | 214.32 |
| Bp | | | |
| <i>S</i> | 27 | 16 | 28 |
| <i>H</i> | 2.62 | 2.36 | 2.93 |
| <i>C</i> | 0.144 | 0.114 | 0.078 |
| <i>J</i> | 0.80 | 0.85 | 0.88 |
| TOTAB | 162.90 | 64.30 | 120.03 |

S: total species richness;
H: Shannon diversity index;
C: Simpson dominance index;
J: evenness; TOTAB: total abundance of the species (see “Methods”)

bootstraps there were no significant inter-annual differences for any of the examined parameters (in each cases, at least $P > 0.121$ after Mantel test comparisons on the data matrices). As for Bp, there were also no significant inter-annual differences for the parameters *S*, *H* and *J* (at least $P > 0.121$ at Mantel test), but for *C* ($P < 0.032$). Thus, the only significant difference between Rp and Bp was that, after bootstrapping, *C* was observed to vary significantly among years in Bp but not in Rp. As for the differences between Rp and Bp, these were statistically significant and non-random with regard to the parameter ‘TOTAB’ ($P < 0.014$), but not for *S*, *H*, *C* and *J* (in all cases, at least $P > 0.365$).

At community level, the β_T -turnover index in the period of study showed higher values in Bp respect to Rp (Table 3), but these differences may be in part a by-product of chance. Unfortunately, as we lack of adequate replicates, we could not test for it.

Guild and species level

Forest *s.l.* species richness was lower in Rp as compared to Bp in all the sampling years (in 2002, the difference was statistically significant; Table 4). Among the 3 years, forest species richness did not show significant differences in both Rp ($\chi^2 = 0.01$, $df = 2$, $P = \text{NS}$) and in Bp ($\chi^2 = 5.28$, $df = 2$, $P = \text{NS}$). After bootstrapping ($n = 5,000$ permutations), it resulted that, however, the lesser *S* values (and, consequently, also the *S_f* and *S_e* values; see Table 4) observed in 2002 were possibly produced by chance (Mantel test, at least $P = 0.360$).

Edge species richness did not show a significant difference between Rp and Bp in all the sampling years, but values are always higher in Bp respect to Rp (Table 4). The edge species richness did not show a significant difference in either Rp

Table 3 β_T -turnover index (Wilson and Shmida, 1984) calculated for the whole period of study (2001–2003) in residual and burnt pinewood

| | Rp | Bp |
|--------|-------|-------|
| Total | 0.053 | 0.091 |
| Forest | 0.043 | 0.027 |
| Edge | 0.091 | 0.22 |

Values are at community and guild level (forest *s.l.* and edge species)

Table 4 Species richness and abundance of bird communities in 3 years of study

| Parameter | 2001 | | | 2002 | | | 2003 | | |
|-----------|------|------|----------|-------|-------|----------|-------|-------|----------|
| | Rp | Bp | χ^2 | Rp | Bp | χ^2 | Rp | Bp | χ^2 |
| S | 28 | 27 | 0 | 29 | 16 | 3.20 | 26 | 28 | 0.02 |
| S_f | 21 | 18 | 0.10 | 23 | 7 | 7.50** | 23 | 17 | 0.06 |
| S_e | 7 | 9 | 0.06 | 6 | 9 | 0 | 3 | 11 | 3.50 |
| TOTAB | 226 | 163 | 9.84** | 244.3 | 64.3 | 108.84** | 214.3 | 120 | 26.03** |
| ABf | 131 | 68.6 | 19.12** | 117.1 | 17.16 | 72.95** | 112.9 | 35.73 | 39.01** |
| ABe | 70 | 78.6 | 0.62 | 92.87 | 45.71 | 1.33 | 71.44 | 78.58 | 0.44 |

Symbols: Se = total, forest and edge species richness; TOTAB, ABf, ABe: respectively, total, forest and edge abundance of species. χ^2 test (1 d.f.; Yates correction) among variables in residual (Rp) and burnt (Bp) pinewood

** $P < 0.01$

($\chi^2 = 1.62$, $df = 2$, $P = \text{NS}$) or Bp ($\chi^2 = 0.29$, $df = 2$, $P = \text{NS}$) among the 3 years. This is also clearly verified by bootstraps and then application of Mantel test ($P < 0.001$).

The total abundance of forest species was always remarkably lower in Bp than in Rp (Table 4). Among the three study years, the abundance of forest species did not change noticeably in Rp ($\chi^2 = 1.50$, $df = 2$, $P = \text{NS}$), but in Bp ($\chi^2 = 33.51$, $df = 2$, $P < 0.01$). The same result was also observed by using Mantel test after 5,000 bootstraps ($P < 0.01$).

The differences in total abundance of edge species between Bp and Rp were not significant (Table 4). Among the 3 years of study, the abundance of the edge species did not change noticeably in Rp ($\chi^2 = 4.19$, $df = 2$, $P = \text{NS}$), but in Bp ($\chi^2 = 10.64$, $df = 2$, $P < 0.01$), and the same patterns were confirmed by Mantel test on bootstrapped data (for Rp, $P > 0.451$, for Bp, $P < 0.001$).

Overall, the edge species tended to increase in richness and evenness from Rp to Bp, contrary to the forest species that, following a reduction in richness, did not show a reduction in evenness (Fig. 2).

Edge species showed, in both Bp and Rp, β_T -turnover values higher than the forest species. In Bp, edge species showed the highest values of turnover among the 3 years (Table 3).

At the species level, most of the species showing a significant decrease in median abundance comparing Rp to Bp (Table 5) were designed as forest species in an a priori selection (Table 1). Vice versa, the species showing a significant increase (Table 5) coincided with an a priori classification of edge species (Table 1). An exception is relative to *Sylvia cantillans*, designed as edge species, that did not show a significant decrease in Bp respect to Rp (Tables 1 and 3). *Carduelis carduelis* and *Emberiza cirlus*, edge/open habitat species, did not show a predictable trend between Rp and Bp (Table 3).

Discussion

Community level

At the community level, the assembly structure of breeding birds was apparently influenced by the fire event at our study area. Although the number of species did

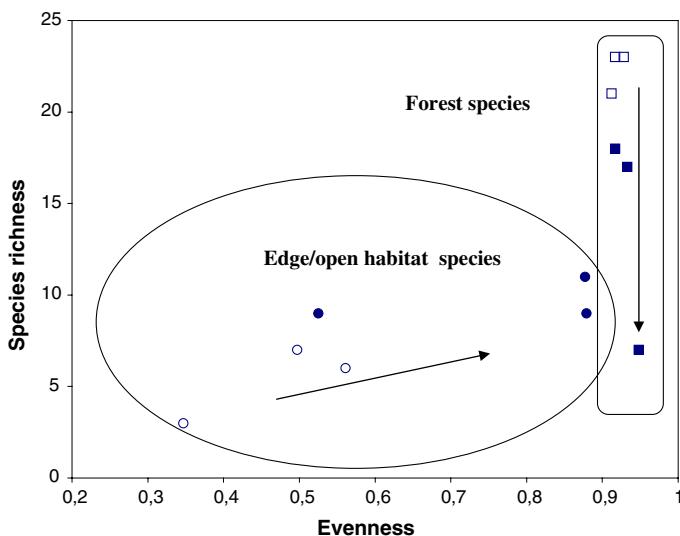


Fig. 2 Species richness (S)/evenness (J) diagram. Squares: forest species; circles: edge species. In white: Rp; in black: Bp. Rows are indicative (Rp towards Bp)

not show significant differences among years inside pinewoods and between burnt and residual plots in each year, edge habitats and spatial heterogeneity at the landscape level, consequently to fire event, induced a turnover in species, as confirmed by β_T index. This evidence is consistent with literature data showing that habitat heterogeneity at the landscape scale appears a key factors in maintaining bird diversity (included β) in fire-driven Mediterranean landscapes (Bock and Lynch 1970; Bendell 1974; Herrando et al. 2003; Brotons et al. 2004).

Considering the total abundance (TOTAB) parameter, our study provided evidence of a fire effect on the whole communities. Indeed, the residual pinewoods always showed a higher total abundance as compared to the burnt pinewood. Structural factors linked to vegetation may explain the values obtained: alteration of the shrub, tree and canopy layers, may cause a reduction in the total resource availability, and this could induce in turn a decrease in total bird abundance (MacArthur and MacArthur 1961). During the 3 years of study, in the burnt pine-wood the oscillations in total abundance are due to opposite patterns obtained for the selected guild (forest *s.l.* and edge). Significant oscillations in total abundance of the species and in species richness (see β_T - turnover) among the 3 years were obtained for burnt pinewood suggesting more dynamic conditions (e.g. fluctuation of resources) compared to residual pinewood (see Moreira et al. 2003).

Apart from the total abundance parameter, all the other parameters examined during the present study revealed no differences between burnt and control (=residual) plots or, when there were some differences, these were in part explained by the chance effects after our Monte Carlo procedures of analysis. This fact suggests that, despite the large scale and presumed catastrophic effects of the fire at our study area, most of the apparent fire effects on the avian communities were either of little impact (i.e. very local) or just apparent. Thus, it seems that the fire consequences at our bird community level were relatively moderate, and that the ‘biodiversity

regrowth' may be easier and more flexible than expected in the case of this potentially (and apparently) devastating fire event.

Guild and species level

The consequences of the fire event were more evident at the guild-level than at the community-level. The change in the habitat structure in the burnt pinewood determined evident changes in richness and abundance of the selected guilds (forest versus edge species).

At the species richness level, the number of forest *s.l.* species was lower in burnt respect to residual pinewood across the whole study period. In any case, contrary to forest *s.l.* species, edge species showed a slight increase in species richness but an evident increase in evenness from residual to burnt pinewoods (Fig. 2). Although edge species richness did not show significant differences between residual and burnt pinewoods, in the entire period of study their abundance values significantly oscillated.

Table 5 Results of one-tailed Wilcoxon paired test among median abundance of the species in residual (Rp) and burnt (Bp) pinewood

| Species | Rp, median | Bp, median | T | n | P | e/f | +/- |
|--------------------------------|------------|------------|------|---|-------|-----|-----|
| <i>Streptopelia decaocto</i> | 0 | 1.43 | 0 | 6 | <0.01 | e | + |
| <i>Streptopelia turtur</i> | 8.57 | 1.43 | 0 | 9 | <0.01 | f | - |
| <i>Picus viridis</i> | 4.29 | 1.43 | 0 | 8 | <0.01 | f | - |
| <i>Dendrocopos major</i> | 4.29 | 1.43 | 1 | 8 | <0.01 | f | - |
| <i>Picoides minor</i> | 2.86 | 0 | 0 | 9 | <0.01 | f | - |
| <i>Motacilla alba</i> | 0 | 2.43 | 0 | 9 | <0.01 | e | + |
| <i>Troglodytes troglodytes</i> | 15.71 | 5.71 | 0 | 9 | <0.01 | f | - |
| <i>Erithacus rubecula</i> | 4.29 | 1.43 | 0 | 9 | <0.01 | f | - |
| <i>Luscinia megarhynchos</i> | 2.86 | 1.43 | 0 | 9 | <0.01 | f | - |
| <i>Turdus merula</i> | 10 | 5.71 | 0 | 7 | <0.01 | f | - |
| <i>Sylvia melanocephala</i> | 2.86 | 7.14 | 0 | 9 | <0.01 | e | + |
| <i>Sylvia atricapilla</i> | 12.86 | 4.29 | 0 | 9 | <0.01 | f | - |
| <i>Sylvia cantillans</i> | 1.43 | 0 | 4.5 | 6 | ns | e | (-) |
| <i>Phylloscopus collybita</i> | 1.43 | 0 | 0 | 7 | <0.01 | f | - |
| <i>Regulus ignicapillus</i> | 2.86 | 0 | 0 | 9 | <0.01 | f | - |
| <i>Muscicapa striata</i> | 5.71 | 0 | 0 | 7 | <0.01 | f | - |
| <i>Aegithalos caudatus</i> | 7.14 | 0 | 1 | 9 | <0.01 | f | - |
| <i>Parus caeruleus</i> | 10 | 2.86 | 0 | 9 | <0.01 | f | - |
| <i>Parus major</i> | 10 | 5.71 | 0 | 8 | <0.01 | f | - |
| <i>Sitta europaea</i> | 15.71 | 1.43 | 0 | 9 | <0.01 | f | - |
| <i>Certhia brachydactyla</i> | 7.14 | 2.86 | 3 | 9 | <0.01 | f | - |
| <i>Garrulus glandarius</i> | 2.86 | 1.43 | 1.5 | 6 | ns | f | (-) |
| <i>Oriolus oriolus</i> | 1.43 | 0 | 0 | 9 | <0.01 | f | - |
| <i>Sturnus vulgaris</i> | 58.57 | 20 | 3 | 8 | <0.05 | f | - |
| <i>Passer italiae</i> | 0 | 5.71 | 0 | 9 | <0.01 | e | + |
| <i>Fringilla coelebs</i> | 12.86 | 1.43 | 0 | 9 | <0.01 | f | - |
| <i>Serinus serinus</i> | 0 | 2.86 | 0 | 6 | <0.01 | e | + |
| <i>Carduelis chloris</i> | 2.86 | 8.57 | 12.5 | 9 | ns | e | (+) |
| <i>Carduelis carduelis</i> | 5.71 | 5.71 | 12.5 | 8 | ns | e | - |
| <i>Emberiza cirlus</i> | 1.43 | 1.43 | 15 | 8 | ns | e | - |

Species with $n < 6$ were not considered. A priori selection of the species in guilds (forest *s.l.* and edge) and a posteriori differences between pinewoods (decreasing [-], or increasing [+]) is indicated (among brackets, non-significant values)

After the fire, edge-guild developed their structure from a low species richness and low evenness to a richer community, as confirmed by dominance index (higher the index, more total frequency is concentrate in a low number of species; Simpson 1949). This index shows an increase from 2001 to 2003 in residual pinewood, and a decrease in the burnt plot. β_T -turnover index highlighted the role of edge species as a new component of the whole bird community structure subsequently to the fire event: in all the 3 years of study, its values were highest in edge species and in burnt pinewood.

The abundance of species subdivided by ecological guild is a parameter more sensitive than species richness at community or guild level. A significant oscillation in the abundance patterns for edge and forest *s.l.* species was observed in burnt pinewood during the study period 2001–2003. This was not observed in residual pinewood during the same period suggesting differences in terms of stability between pinewoods (old-mature versus highly disturbed, more dynamic: see turnover). These guild-related changes in abundance may explain the oscillations in total abundance values.

In all the 3 years of study, forest *s.l.* species were more abundant in the residual pinewood. These species showed in 2002 and in 2003 a reduction of abundance in burnt pinewood, linked to the habitat transformation and reduction of shrub layer and to an increase of spatial heterogeneity (e.g. see Webb et al. 1975; Taylor and Barnmore 1980; Blake 1982).

The reduction of forest *s.l.* species richness and abundance in burnt pinewood could be explained, other than by vegetation-structural causes, also by trophic reasons: many forest species are insectivorous and could be influenced by a reduction in invertebrate biomass in burnt pinewood (Guerrieri and Castaldi 2003). Vice versa, edge species were more abundant in burnt pinewood than in residual pinewood. The reduction and disappearance of the tree/shrubby component and the increase of (resource) patchiness in burnt pinewood could explain the increase of richness and abundance of edge species (Bellamy et al. 1996; Herrando et al. 2003).

The destruction of the canopy as a consequence of fire produced an impact on the trophic and reproductive habitat used by the forest species (see Guerrieri and Castaldi 2003). At structural level, mature pinewood might represent a surrogate habitat of the natural complex, well structured habitats (such as the deciduous mixed woods of *Quercus robur* and *Populus alba*) which were distributed along the coast line before the anthropic transformation of the Roman hinterland (first half of the 20th century). This surrogate habitat is suitable for many bird species of conservation concern at a regional scale (e.g. *Picoides minor*; Boano et al. 1995; Biondi et al. 1999) and the catastrophic fire event could have determined a negative response for them.

Although the fire evidently disturbed the habitat of forest *s.l.* species, a role at trophic and reproductive levels of the dead wood mass is yet assumable, at least for hole-nesting birds (e.g. specialists as Piciformes, *Sitta europaea* and generalists as *Sturnus vulgaris*) that, although showing a significant decrease in abundance, persisted in the burnt pinewood (except for *Picoides minor*). Indeed, the largest size-class of the trunks (diameter > 38 cm) showed no significant differences in the two habitat types, pointing out to a limited impact of the fire on the structural component of the tree vegetation (i.e. wood biomass). Therefore, forest interior species could experiment a lag effect in decreasing their richness and abundance, induced from the availability of this resource (dead wood mass) in the burnt pinewood. In this sense, the decrease of the forest bird component could be relaxed in a longer time than in

our study (see relaxation effect; Lomolino 2000), and the timespan covered by our research represents a fraction of the whole succession following fire.

Habitat transformation following fire acted on the breeding bird communities by altering the qualitative and quantitative species composition: at community level by increasing the total species richness (but in a less strong way than predictable, given that many other parameters remained practically unaffected) and, at the guild level, by decreasing the forest bird richness and abundance, while increasing edge bird richness, abundance and evenness.

An analysis *a posteriori* (at the species level) largely confirmed the selection made *a priori* of the two selected ecological guilds. Most of the species showing a significant decrease in median abundance between residual and burnt pinewoods were assigned *a priori* to the forest *s.l.* species; the contrary appeared as for those species whose frequency increased after the fire treatment (i.e. coinciding to edge/open habitat species).

The fire event reduced strongly the habitat availability for forest species as well as for the species which are linked to the shrubby layer in Mediterranean forest and ecotones. Catastrophic fires could transform abruptly suitable woodlands (i.e. pinewoods) in unsuitable open habitat, so decreasing the habitat availability also for several edge species.

Overall, our study provided evidence that, in order to investigate the effects of fire catastrophes on birds, the guild approach seems more exhaustive than the taxonomic community approach, where intrinsic confounding trends are present (Verner 1984).

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Indicators for plant species richness in pine (*Pinus sylvestris* L.) forests of Germany

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Abstract Forestry is obliged to record as well as maintain and/or enhance biological diversity in forests due to national and international agreements. Accordingly, it is necessary to work out methodological approaches for the assessment of biodiversity in forests. In the study presented here, we focus on the total plant species pool (563 vascular plant and bryophyte species) of pine (*Pinus sylvestris* L.) forests in NE Germany to identify indicators for plant species richness. We distinguished several groups like “herb”, “grass-like”, “woody”, “endangered”, and “exotic species”, for which we detected indicators for low (class #1), intermediate (class #2), and high (class #3) species numbers. From a total of 84 species, which were identified by a three-step procedure, most indicators were found for class #3. Only few indicators have been revealed for intermediate species numbers, i.e. class #2. With help of Ellenberg’s ecological indicator values and information on the main occurrence in Central European vegetation types and plant communities, respectively, we characterized the indicator species ecologically. The ecological site preferences of the indicator species in general reflect the fact that species richness is highest in base-rich, light, and anthropogenically disturbed pine forests. On the contrary,

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species-poor forests were revealed by indicators, which mainly occur on acidic sites. It is concluded that a considerable set of indicators for species richness can help facilitate biodiversity assessments in forestry and ecosystem restoration practice.

Keywords Biodiversity assessment · Biodiversity indicators · Bryophytes · Endangered species · Exotic species · Species numbers · Vascular plants

Introduction

Natural and anthropogenic forests cover large areas in many landscapes throughout Central Europe and are of fundamental importance for their functionality, biodiversity, and social as well as economic value. So, forestry is one of the major land uses. As reflected in Article 2 of the Convention on Biological Diversity (CBD 2004), biodiversity has become an important nature conservation objective for all land users in the past decades. Accordingly, forestry is obliged to record as well as maintain and/or enhance biological diversity in forests due to national and international agreements (MTK 1995; Korn et al. 2001; MCPFE 2003; CBD 2004).

Biodiversity can never be entirely described but some of its features measured (Mayer et al. 2002; Zerbe and Kreyer 2006). Its complexity causes problems of measurement in practice (Levin 1997; Wieglob 2003). Despite the existence of various correlates and surrogates to analyze and assess biodiversity (Orlóci et al. 2002; Desrochers and Anand 2004; Magurran 2004; Buckland et al. 2005), the most easily communicated approach in science as well as in practice is species count (e.g. Heywood et al. 1995; Gaston 2000).

Plants are considered a key species group in forest ecosystems because of their contribution to primary productions (Mitchell and Kirby 1989; Barthlott et al. 2000; Haeupler 2000). In addition, the knowledge about their taxonomy, ecology, and spatial distribution is quite extensive, in particular for Central Europe (e.g. Haeupler and Schönfelder 1988; Ellenberg 1996; Ellenberg et al. 2001; Oberdorfer 2001). Compared to various animal groups, plant species can be more easily recorded within biodiversity assessment procedures. For this reason, we focus here on vascular plants and bryophytes for the identification of indicators for plant species richness in forests. Additionally to the objectives of biodiversity science, the identification of biodiversity indicators is an important basis for practical purposes like nature conservation, natural resources management, and natural forest restoration. Indicator species have a long tradition for the assessment and monitoring of ecosystems (Noss 1999).

As natural and anthropogenic pine (*Pinus sylvestris* L.) forests are widely spread throughout NE Germany, we aim at the detection of indicators for plant species richness in this forest type. We analyzed plant species of the moss, herb, and shrub layer as possible indicators and measured biodiversity by species number per plot. We also examined properties of the objects, i.e. the affiliation to groups, such as herb or woody species, bryophytes, exotic and endangered species, and typical woodland species. The hypotheses of our study were: (1) there are plant species among the total species pool, which predict defined ranges of species numbers in pine forests, (2) these indicators can be detected by our approach, and (3) from the indicators identified, ecological site conditions enhancing species richness in those forest ecosystems can be derived.

The proposed approach is not supposed to substitute comprehensive surveys of vegetation. However, selected indicators allow a rapid assessment of forest stands with regard to the probability of finding defined ranges of species numbers (Schmidt et al. 2006). Those assessments can be carried out with a knowledge focused on the selected indicators and can precede extensive surveys accomplished by specialists in botany.

Study area

The study area was the north-eastern German lowland including the federal states Mecklenburg-Vorpommern, Brandenburg, Berlin, and the northern parts of Sachsen and Sachsen-Anhalt (Fig. 1). The geology as well as the climate shows a pronounced gradient from N to S and NW to SE. Geology and geomorphology of the north-eastern German lowland has been formed during the glacial periods (Schmidt 2002). Whereas the more or less loamy soils of the young pleistocene sediments in the northern part of the study area are rich in nutrients, despite of the outwash plains with purely sandy soils, the older pleistocene sediments in the southern part bear nutrient-poor sandy soils.

The climate varies from sub-oceanic at and near the Baltic Sea coast to sub-continental in the SE of the study area (Passarge 1964; Hendel 2002). Thus, the mean annual precipitation with more than 600 mm and the mean annual air temperature with 8.4°C (city of Schwerin, period of measurement 1961–1990) in the north-west of the study area are distinctly different from the mean annual precipitation with less than 500 mm and the mean annual air temperature with 8.7°C in the south (city of Magdeburg, period of measurement 1961–1990; Mühr 2002).

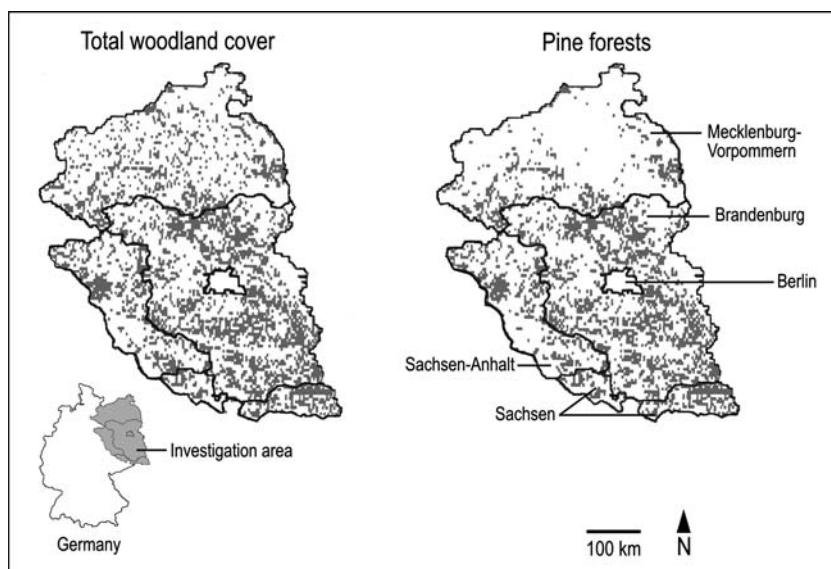


Fig. 1 Pine dominated forests in the investigation area north-eastern German lowland (from Zerbe and Wirth 2006 on the basis of data from Hofmann 1995)

Material and methods

Database

Our database covered pine-dominated forests within the whole range of the geological and climatic gradient of the study area described above. The analyzed database contained data from 22 studies on pine forest ecosystems in the NE German lowland, including in total 1,298 vegetation samples with 563 vascular plant und epigaeic bryophyte species. Due to the species-area-relationship (Arrhenius 1921; Gleason 1922), only vegetation samples with an area size of 400 m² were considered (from a total of 2,289 vegetation samples; cp. Zerbe and Wirth 2006 for the whole database), which provide information on frequency and abundance of plant species. Abundance data were given according to the scale of Braun-Blanquet (1964). The different species synonyms were unified according to Wisskirchen and Haeupler (1998) for vascular plants and Frahm and Frey (2004) for bryophytes.

Species number was used as a feature of biodiversity and analyzed with regard to different groups of plants (Fig. 2). Thus, 14 groups were distinguished (Table 1). The group “herb species” is meant without grass-like species, whereas “herb layer” included the grass-like species. The group “grass-like species” comprised the families Poaceae, Cyperaceae, and Juncaceae. The group of woody plants included phanerophytes (trees), and nanophanerophytes (shrubs). Information on endangered species was taken from the regional (Mecklenburg-Vorpommern, Brandenburg, Berlin, Sachsen, Sachsen-Anhalt) and national Red Lists, compiled by Ludwig and Schnittler (1996). Species assigned to category 1 (critically endangered) to 3 (vulnerable) contributed to the number of endangered species.

The group of typical forest species of vascular plants, i.e. species, which are closely tied to forest ecosystems in their occurrence, was classified according to Schmidt et al. (2003). The following categories were distinguished: W = species of the shrub and herb layer, H = species of the herb layer, 1 = closely tied to forests, 2 = in forests and also in other vegetation types, respectively, and species of open landscapes, i.e. species, which mainly occur in other vegetation types than forests, therefore not assigned to category 1 or 2. Exotic species of vascular plants were categorized following the information given by Wisskirchen and Haeupler (1998). “Archaeophytes” (= species introduced to Central Europe before 1,500 A.D.), “neophytes” (= species introduced to Central Europe after 1,500 A.D.), and “neophytes in the process of naturalization” were classified as “exotic species”. Archaeophytes that leave any doubts concerning a possible affiliation to the indigenous Central European flora were not counted among the exotic plants.

Species number classes and identification procedure for indicators

Our approach used probabilities of predefined ranges of species numbers to occur, if certain species of higher plants and bryophytes were found. For every analyzed species group (Fig. 2) we predefined three classes for the ranges of species numbers. The class #1 included the species-poor stands, class #2 the stands with intermediate species numbers, and class #3 comprised the species-rich stands (Table 1). We strived for equal sample sizes in all three classes.

According to Schmidt et al. (2006), there were three steps for the selection of indicator species:

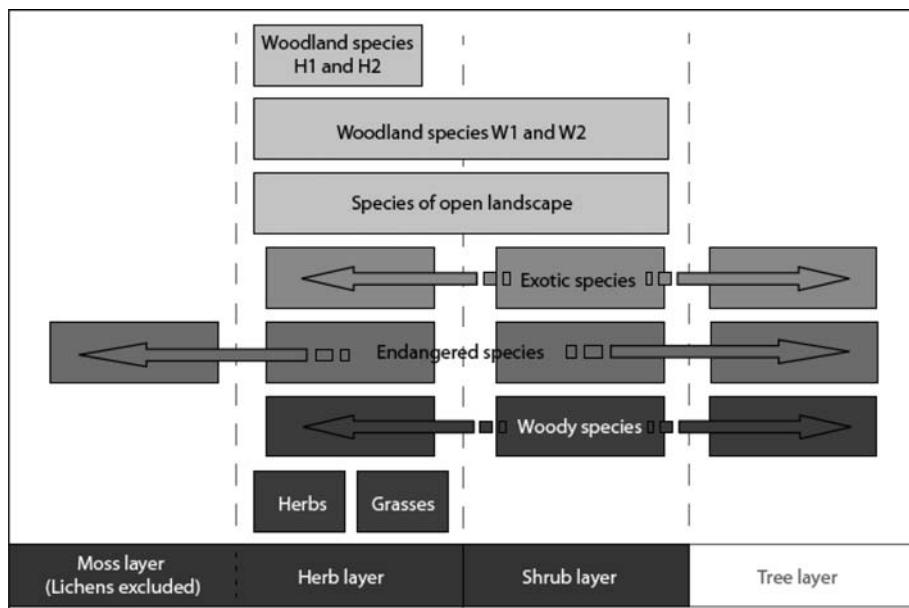


Fig. 2 Plant groups (including the different vegetation layers; cp. Table 1) for which the indicators for species richness have been identified; according to the classification of Schmidt et al. (2003), W = species of the shrub and herb layer, H = species of the herb layer, 1 = closely tied to forests, 2 = in forests and also in other vegetation types, respectively, and species of open landscapes, i.e. species, which mainly occur in other vegetation types than forests, therefore not assigned to category 1 or 2

Table 1 Classes of species numbers for the investigated plant groups (see Fig. 2); SR = range of species numbers in class 1–3, N = number of plots

| | Class #1 | | Class #2 | | Class #3 | |
|---------------------------|----------|-------|----------|-----|----------|-----|
| | SR | N | SR | N | SR | N |
| Moss and herb layer | 4–13 | 411 | 14–21 | 446 | 22–58 | 441 |
| Herb layer | 0–9 | 414 | 10–18 | 449 | 19–55 | 435 |
| Bryophytes | 0–2 | 496 | 3–4 | 444 | 5–11 | 358 |
| Shrub layer | 0 | 375 | 1–2 | 464 | 3–13 | 459 |
| Herb species | 0–2 | 489 | 3–7 | 408 | 8–42 | 401 |
| Grass species | 0–2 | 374 | 3–5 | 569 | 6–12 | 355 |
| Woody species | 1–3 | 325 | 4–6 | 505 | 7–21 | 468 |
| Endangered species | 0 | 552 | 1 | 398 | 2–12 | 348 |
| Exotic species | 0 | 905 | – | – | 1–7 | 393 |
| Species of open landscape | 0 | 1,065 | – | – | 1–9 | 233 |
| Woodland species W1 | 0–1 | 521 | 2–4 | 478 | 5–14 | 299 |
| Woodland species W2 | 0–5 | 441 | 6–10 | 411 | 11–37 | 446 |
| Woodland species H1 | 0–1 | 522 | 2–3 | 342 | 4–14 | 434 |
| Woodland species H2 | 0–4 | 443 | 5–8 | 421 | 9–33 | 434 |

- (1) The first step and crucial criterion was that species x_i should be an indicator if probability $p(c_j|x_i)$ for a class c_j is higher than for the other two classes. $p(c_j|x_i)$ is the probability to be in class c_j if we observed species x_i , that means the probability to be in a site with a species number within the range defined for c_j .

For reasons of practicability, we demanded of an indicator for class j that $p(c_j|x_i) \geq 0.6$, i.e. x_i may be an indicator for class c_j if at least 60% of the plots where we found x_i have a species number within the defined range for c_j . Based on equal sample sizes, this assumption automatically fulfills the demand that x_i should be an indicator for a certain class c_j .

- (2) The second step related to the fact, that the highest probability $p(x_i|c_j)$ has to be in the same class as the maximum $p(c_k|x_i)$ with $j = k$. The value of $p(x_i|c_j)$ is the probability to find species x_i given that we are sampling in class c_j . $p(x_i|c_j)$ corresponds to the degree of species presence. If the maxima of the probabilities $p(c_k|x_i)$ and $p(x_i|c_j)$ were not in the same classes with $k \neq j$, the species x_i was rejected as indicator. In this way, we avoided to use a species as indicator that was more frequent in another class of species numbers than in the class it was an indicator for. This step was only necessary, if the sample sizes in the classes were not equal (cp. Schmidt et al. 2006).
- (3) The last step was to exclude species with a frequency of equal or less than 5% in order to avoid the choice of rare species as indicators.

Additionally, changes in percentage of abundance of indicators were tested. A higher abundance of an identified indicator species in the indicated class supported the practicability of the surrogate. To summarize the approach, we can say that the decisive property for an indicator was the ability to predict a defined range of species numbers c_j with a probability $p(c_j|x_i) > p(c_k|x_i)$, $k \neq j$. The other selection steps facilitated the use of the indicator, avoided the choice of rare species and were therefore necessary for the practicability of the indicator species.

Ecological characterization of the indicators

We characterized identified indicator species with the indicator values (values 1 to 9) by Ellenberg et al. (2001), which give information about the occurrence of plant species in ecosystems along gradients of soil moisture, soil reaction, light, and nitrogen availability. These indicator values are commonly applied, in particular in Europe for ecological site and plant species assessment (e.g. Ellenberg 1996; Dupré and Diekmann 1998; Lawesson et al. 2003). We used only presence-absence values of the concerned species, as recommended by Kowarik and Seidling (1989), for calculating the medians of Ellenberg's indicator values in the classes.

Additionally, the indicator species were grouped according to Oberdorfer's (2001) information on the species' phytosociological range, i.e. the vegetation types and plant communities, respectively, in which the species mainly occur. We distinguished mesophytic grassland, dry and nutrient-poor grassland, mires, broad-leaved forests, forest edges and vegetation on forest clear-cuts, coniferous forests, vegetation of fallow land and fields, heaths, and vegetation of open water and floodplains.

Results

Identified indicators for species richness

Within the distinguished plant groups, different ranges of species numbers have been defined for the classes #1 to #3 (Table 1). The lowest number within class #1 with no

species at all (“0”) is given for the group “shrub layer”, “species of the open landscape”, “endangered species”, and “exotic species”. The ranges of species numbers within the three classes vary from 1 to 36. The maximal species number per plot (400 m^2) in the investigated pine forests is 58, considering all vascular plants and bryophytes together.

From the total pool of 563 vascular plant and bryophyte species, a minimum of 13 (ca. 2%, “endangered species”) and a maximum of 44 (ca. 8%, “exotic species”) indicator species could be identified (Table 2). Numbers of indicators within the groups mostly ranged between 20 and 40. In general, the identified species indicated class #3, i.e. highest species numbers. Only with regard to the groups “bryophytes”, “exotic species”, “species of open landscapes”, and “endangered species”, a considerable number of indicators for class #1 (lowest species numbers) could be found. Only few indicators were recorded for class #2, i.e. intermediate species numbers. For this class, a maximum of four indicator species were revealed for the group “grass species”. These species are *Galeopsis bifida* et *tetrahit* (some of the species have to be summed up because of uncertainty of determination as recommended by Wildi et al. 1996), *Galium saxatile*, *Senecio sylvaticus*, and *Teucrium scorodonia*.

Within the group “moss and herb layer” most intra-indicators were found for class #3 (Table 3). These were indicator species, which belong to the plant group for that they were indicators (e.g. exotic species as indicators for plant species richness within the group of “exotic species”). Nearly no intra-indicators could be revealed for the classes #1 and #2.

In total, 84 indicators were identified (see Supplementary Table). Within this list of indicators, the same species could be a different indicator in the various vegetation layers. *Betula pendula* et *pubescens* (see annotation above for *Galeopsis bifida* et *tetrahit*), for example, is an indicator for low species numbers (class #1) of “exotic species” and “species of open landscapes” and for high species numbers (class #3) in the group “shrub layer”. Among the identified indicators were 37 herbs (without grasses), 13 grasses (e.g. *Anthoxanthum odoratum*, *Calamagrostis epigejos*, *Carex pilulifera*, *Holcus mollis*, *Luzula pilosa*, *Molinia caerulea*), 15 woody species (e.g. *Fagus sylvatica*, *Frangula alnus*, *Juniperus communis*, *Picea abies*, *Prunus serotina*,

Table 2 Numbers of indicators for plant species richness, identified for the investigated plant groups by means of three selection steps (for W1, W2, H1, and H2 see caption of Fig. 2)

| Species group | Total | Class #1 | Class #2 | Class #3 |
|---------------------------|-------|----------|----------|----------|
| Moss and herb layer | 35 | 1 | 0 | 34 |
| Herb layer | 37 | 3 | 0 | 34 |
| Bryophytes | 27 | 19 | 0 | 8 |
| Shrub layer | 23 | 1 | 0 | 22 |
| Herb species | 37 | 7 | 1 | 29 |
| Grass species | 26 | 1 | 4 | 21 |
| Woody species | 35 | 2 | 0 | 33 |
| Endangered species | 13 | 12 | 0 | 1 |
| Exotic species | 44 | 28 | — | 16 |
| Species of open landscape | 43 | 38 | — | 5 |
| Woodland species W1 | 20 | 9 | 0 | 11 |
| Woodland species W2 | 38 | 3 | 0 | 35 |
| Woodland species H1 | 35 | 9 | 0 | 26 |
| Woodland species H2 | 36 | 4 | 1 | 31 |

Table 3 Number of intra-indicators, i.e. indicator species which belong to the group for that they are indicators, e.g. exotic species as indicator for plant species richness within the group “exotic species” (“endangered species” omitted)

| Species group | Class #1 | Class #2 | Class #3 |
|---------------------------|----------|----------|----------|
| Moss and herb layer | 1 | 0 | 33 |
| Herb layer | 0 | 0 | 32 |
| Bryophytes | 0 | 0 | 7 |
| Shrub layer | 0 | 0 | 6 |
| Herb species | 1 | 1 | 24 |
| Grass species | 0 | 0 | 6 |
| Woody species | 0 | 0 | 6 |
| Exotic species | 0 | – | 3 |
| Species of open landscape | 0 | – | 0 |
| Woodland species W1 | 0 | 0 | 7 |
| Woodland species W2 | 0 | 0 | 23 |
| Woodland species H1 | 0 | 0 | 11 |
| Woodland species H2 | 0 | 1 | 20 |

Sorbus aucuparia) and 12 bryophytes (e.g. *Brachythecium rutabulum*, *Dicranella heteromalla*, *Hypnum cupressiforme*, *Leucobryum glaucum*, *Polytrichum formosum*).

As mentioned above, most indicators were found for class #3. For example *Agrimonia eupatoria*, *Euphorbia cyparissias*, *Polygonatum odoratum*, and the *Rubus* species indicate class #3 in various plant groups. In general, only few species like the bryophytes *Dicranum polysetum*, *Leucobryum glaucum*, *Pohlia nutans*, *Ptilidium ciliare* and the dwarf shrub *Vaccinium vitis-idaea* are indicators for class #1 with the lowest species numbers per plot. However, within the groups “bryophytes”, “exotic species”, “endangered species”, and “species of open landscapes” a relatively large number of indicators revealed class #1.

Site preferences of the indicators

With the calculation of Ellenberg’s indicator values for specific site demands of the plant species for light, moisture, soil reaction, and nutrient availability, trends are shown in Fig. 3. Due to the low number of indicators for class #2 (Table 2), only results for class #1 and #3 were presented with regard to selected plant groups. Those plants, for example, which indicated a low number of bryophyte species (class #1 with 0–2 species) can mainly be ecologically characterized as species, which have a relatively high demand for light and base-rich soils (Ellenberg values from 6 to 8). Intermediate soil moisture favors the growth of these species (values 4 and 5). On the contrary, most species which indicate high numbers of bryophyte species (class #3) grow on very acidic (mostly value 2) and dry to moderately dry sites (values 2 to 4). This corresponded to the indicators for low numbers (class #1) of “endangered species”, at least for the light demand (Fig. 4). Indicators for low species numbers (class #1) of “endangered species” are growing preferably on very acidic sites (Ellenberg value 2).

Those species, which indicated pine stands with no occurrence of exotic species at all (class #1), are mainly growing in relatively light forests (values 5 to 8) on acidic and nutrient-poor sites (Fig. 3: values 1 to 4). Opposed to this, the forest sites where up to 7 exotic species occur (e.g. *Mahonia aquifolium*, *Prunus serotina*, *Quercus rubra*, and *Robinia pseudoacacia*), mainly are richer in bases and nutrients.

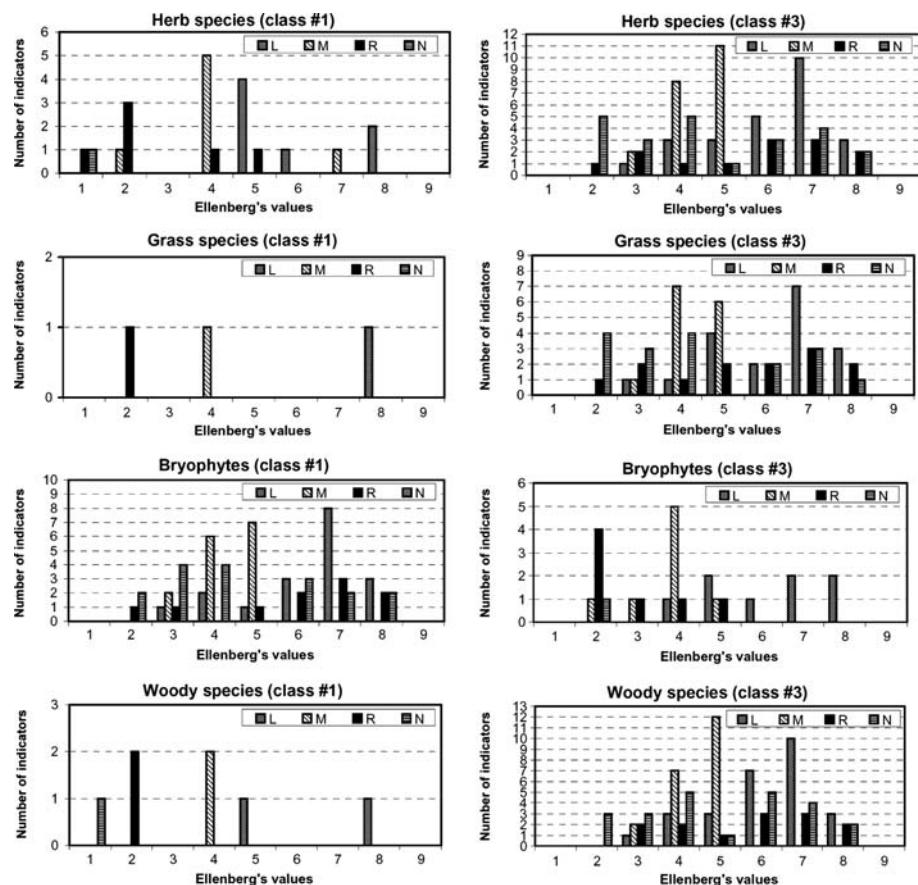


Fig. 3 Ellenberg's indicator values for light (L), moisture (M), soil reaction (R), and nutrient availability (N) for indicator species for classes #1 and #3 within selected plant groups

Indicators for pine forests with a rich herb flora (class #3), mostly grow on sites relatively rich in bases under a light canopy (Ellenberg values 6 to 8). The nutrient demand of these species shows no distinct trend (Fig. 3). The same holds true for species, which indicated high numbers of grass and woody species (class #3). In general, they have a high light demand and grow on base-rich sites. In contrast, indicators for low species numbers (class #1) of herbs prefer acidic to moderately acidic and moderately dry forest sites (indicator value < 5).

Species, which indicated a high number of typical woodland species (woodland species H1 and H2, class #3), in general have a high light demand. With regard to the soil reaction and the nutrient availability, no distinct trend could be revealed (Fig. 3).

Indicators for the three classes have been characterized with regard to their main occurrence in different vegetation types and plant communities, respectively (Fig. 4). For those plants, which indicated high species numbers (class #3) in the herb and moss layer, it could be shown that they mainly occur outside of forests, such as mesophytic and dry grassland, fallow land, and forest edges (88%). This also holds

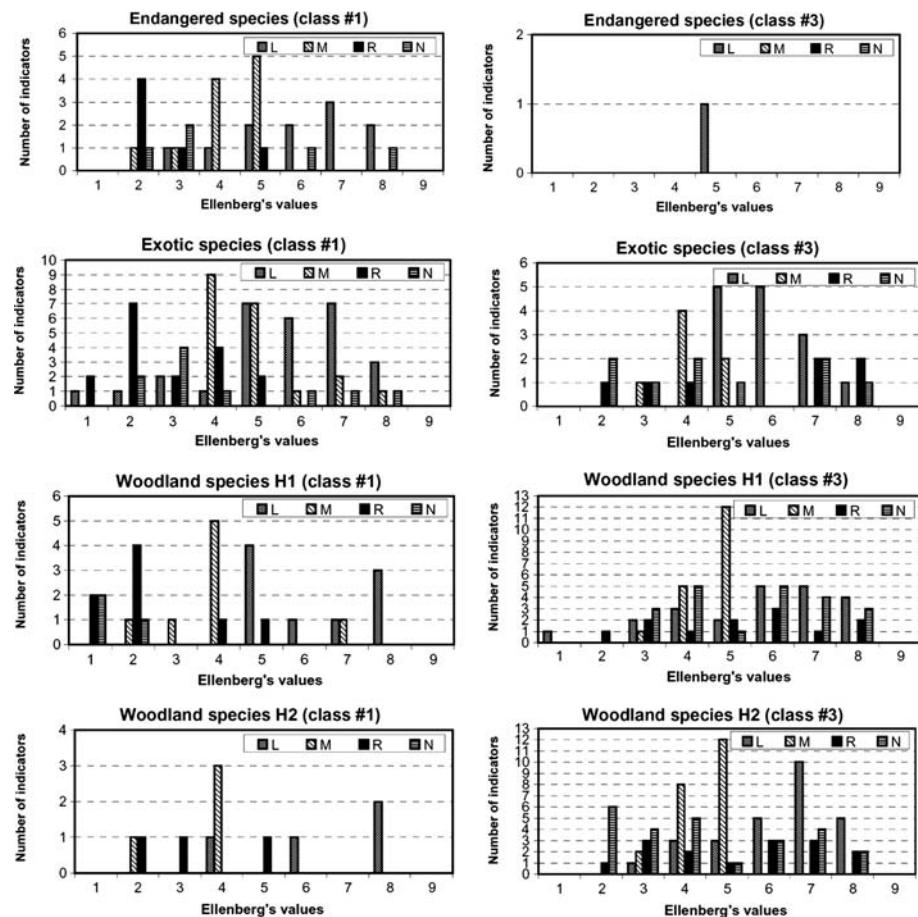


Fig. 3 continued

true for the indicators of high numbers of herb species. On the contrary, the plants, which indicated low species numbers (class #1) of herbs, mainly are found in forests, i.e. broad-leaved as well as coniferous forest stands, and heaths (86%).

Plants which indicate low bryophyte species numbers (class #1) mostly grow on sites outside of forests, like meadows, heaths, and forest edges (about 89%). However, the percentage of indicators for high numbers of bryophyte species (class #3), which are typical forest species, was relatively high with 8. Indicators for pine forests without any exotic species (class #1) mostly belong to the group of species mainly growing in forests (89%). On the contrary, those indicators for high species numbers (class #3) of exotics are mainly found outside of forests (88%).

Discussion

There are several approaches to measure and assess biodiversity by indicators. In general, indicators for biodiversity are pre-selected and than tested for the

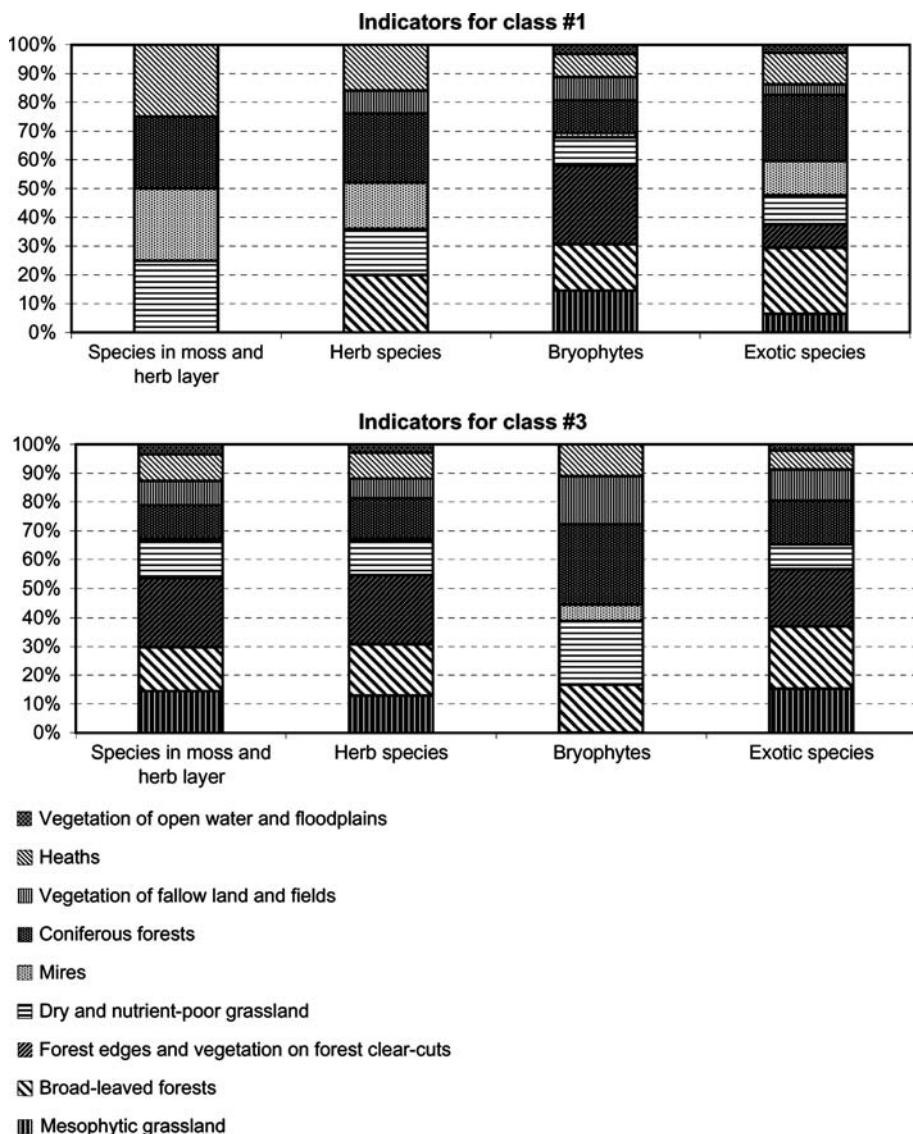


Fig. 4 Indicators for plant species richness in pine forests characterized by their main occurrence in different vegetation types and plant communities, respectively

relationship between the occurrence of indicators and biodiversity. These species are known as focal, target, keystone, umbrella, or flagship species (e.g. Lambeck 1997; Ferris and Humphrey 1999; Noss 1999; Carignan and Villard 2002). They often play a role for practical purposes like nature conservation or ecosystem monitoring. Kreyer and Zerbe (2006) for example, proved a relationship between the occurrence of short-lived tree species (*Betula* spec., *Frangula alnus*, and *Sorbus aucuparia*) in forest ecosystems and increased species numbers. Consequently, they identified

short-lived tree species as target species for the assessment of biodiversity, in particular in anthropogenic coniferous forests.

Our approach focused on the total species pool (563 vascular plant and bryophyte species) along the whole ecological range of pine forests in NE Germany, without pre-selecting species. Consequently, the hypotheses that (1) there are indicators for species richness within the total species pool of pine forests and that (2) we can detect them by our approach have been testified here. Only with regard to the intermediate species numbers (class #2), our approach did not show clear tendencies, because of the overall small number of indicators. So, we could not separate indicators for intermediate species richness to a large extent. However, most indicator species were detected for the species rich class #3. This is partly due to the larger species pool in species-rich stands.

The identified indicators clearly revealed ecological characteristics of those pine forests, in which a large number of vascular plant and bryophyte species can be expected (class #3) and vice versa (class #1). From the results on bryophyte richness in pine forests, it can be concluded that most bryophyte species can be found on acidic forest sites (Fig. 3). On the contrary, light forests on sites rich in bases only bear low species numbers of bryophytes. Most bryophytes in pine forests are susceptible to competition due to their growth form. Thus, e.g. the bryophytes *Hypnum cupressiforme*, *Lophocolea* spec., *Plagiomnium* spec., and *Plagiothecium* spec. are creeping close to the forest floor over the needle litter in pine forests (Frahm and Frey 2004).

It can be derived from the results on the ecological characterization of the indicators for pine forests rich in herb, grass, and woody species that these forests are light with a relatively open canopy. No dense cover of the shrub and lower tree layer for example with broad-leaved trees is expected here. Additionally, soils are relatively rich in bases. The relationship between nutrient availability and species richness has also been revealed by Leuschner (1999) for forest communities in Central Europe. On the basis of the large data set from Oberdorfer (1992) he showed an increase of species numbers in the herb layer with increasing base supply.

The total number of exotic species in Central European forests is, in general, rather low (e.g. Lohmeyer and Sukopp 1992; Zerbe and Wirth 2006) compared, for example, to non-forest ecosystems like settlements (e.g. Pyšek 1989 and 1993; Sukopp 1998; Zerbe et al. 2003) and strongly disturbed habitats outside of settlements like fields (Kowarik 2003). In the investigated forests, relatively high numbers of exotic species have to be considered on sites rich in bases.

It has been revealed that moderate disturbance of forests might increase species richness (e.g. Kessler 2001). Species, which are typical for open landscapes with e.g., pastures and meadows or forest edges, thus can find suitable living conditions on those sites disturbed by forest management (e.g. occurrence of “safe sites” for the rejuvenation of species; Urbanska 1992). Additionally, the anthropogenic spread of those species is enhanced along forest paths and streets (e.g. Schmidt and Weckesser 2001; Westphal 2001; Oheimb 2003). Increased species richness in disturbed forests compared to undisturbed forests is in accordance with the intermediate disturbance hypothesis (Connell 1978; Hobbs and Huenneke 1992). On a regional scale, Deutschewitz et al. (2003) concluded that species richness increases with moderate levels of natural and/or anthropogenic disturbances. In our study, many of the plants, which indicated high species diversity, were commonly occurring in the open landscape (Fig. 4).

Conclusions

With our approach we identified mostly indicators for low as well as high species richness in pine forests of the north-eastern German lowland. From a practical point of view, most indicator species are easily to determine in the field. The indicator species were herbs and woody species to a large extent. This holds also true for most of the bryophytes. With the exception of the two liver mosses *Lophocolea heterophylla* and *Ptilidium ciliare*, all bryophytes can be easily recorded on the forest floor.

It can be concluded that pine forests with a low canopy cover, on base-rich soils and moderately disturbed by forestry are species-richer than pine forests with dense canopies (in particular young forest stands, plantations and/or stands with a dense cover of the shrub and lower tree layer) on very acidic sites. However, this can only be derived from the groups we have investigated. For other groups, like lichens, the results can be different. So, most lichen species in pine forests of NW Germany are revealed for sites which are acidic and have a very low nutrient availability (cp. forest survey from Heinken 1995 in NW Germany). This often is a consequence of former over-utilization of forest sites (Zerbe et al. 2000).

The conversion of anthropogenic into natural forests has become a major task of forestry throughout Europe (Olshoorn et al. 1999; Klimo et al. 2000; Zerbe 2002; Spiecker 2003). With the help of the identified indicators for species richness, specific development objectives for pine stands in NE Germany can be derived:

- (1) Formerly pure pine stands can be most probably developed towards mixed-species forests on those sites, where indicators reveal a high number of woody species. These indicators are, e.g. *Brachypodium sylvaticum*, *Convallaria majalis*, *Hieracium lachenalii*, and *Polygonatum odoratum*.
- (2) Pine forests rich in species of the herb and moss layer are detected by, e.g. *Campanula rotundifolia*, *Euphorbia cyparissias*, *Galium verum*, *Hieracium* div. spec., and *Veronica chamaedrys*. These pine forests can considerably contribute to biodiversity within managed forests, thus playing a major part within the certification of sustainable forest use (e.g. Forest Stewardship Council 2003). However, with regard to species and habitat protection, pine stands with relatively high numbers of endangered species cannot be detected by our approach. Only *Picea abies* (shrub layer), a species which is anthropogenically widespread in NE Germany, indicates endangered species.
- (3) With regard to possible problems caused by invasive species in forests (e.g. Starfinger 1997; Knoerzer 1999; Kowarik 2003; Zerbe and Wirth 2006), pine forests with a considerable number of exotic species can be identified by our indicators, for example by *Agrimonia eupatoria*, *Cerastium holosteoides*, *Prunus serotina* (intra-indicator), and *Torilis japonica*. These forest stands should in particular be monitored in order to observe the development and spread of exotic species.

It can be concluded that a set of indicators for species richness can help facilitate biodiversity assessments in forestry and ecosystem restoration practice.

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The social negotiation of nature conservation policy: conserving pinewoods in the Scottish Highlands

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Abstract This paper examines the social and cultural processes through which conservation policy is derived. Focusing on the management of pinewoods in Abernethy Forest, Scotland, it explores the cultural politics involved in developing appropriate management practice. Calling upon participant observation, semi-structured interviews with site managers and the analysis of texts, it traces the gradual moves from a policy of minimum intervention towards more complex management regimes. The paper explores the social construction of the forest's naturalness that underpinned the early policy of minimum intervention and then the ways that the forest was reconstructed as the managers debated the merits of minimum intervention and the degree to which they should intervene. The paper illustrates how managers have considered different forms of intervention and how they have tried to balance their concern with the naturalness of the forest with a need to intervene on behalf of particularly important species. It highlights the importance of conservationists' culturally derived understandings of nature and suggests that an awareness of these cultures of nature is vital if conservationists are to develop robust policies.

Keywords Conservation · Nature · Pinewoods · Scotland · Social construction · Naturalness

Introduction

In deciding how to act conservationists have to grapple with some difficult and enduring questions. What is natural? Are people a part of, or apart from, nature? How far should people intervene in and shape natural systems? Such questions pose knotty philosophical problems that must be addressed every time decisions have to be made about how best to conserve nature. Yet answers to these questions are as

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varied as conservationists themselves. So how does one policy, one way of conserving nature, come to be understood as more appropriate than another?

It is the contention of this paper that conservation policy is socially and culturally negotiated. Although conservation has come to be understood as an applied science, it is still about so much more than science alone. As Adams (2003, p. 96) makes clear ‘scientific ideas about ecosystems, or ‘biodiversity’, are tightly interwoven with broader ideas about natural beauty, naturalness or the desirability (and desirable limits) of ecological change’. Despite the important role that science plays in shaping conservation practice, policy is equally shaped by socially and culturally produced ideas of nature that become interwoven within the social world of conservation itself.

The paper examines this social and cultural negotiation of nature conservation policy by focusing on the detail of one example of conservation management: the management of pinewoods in Abernethy Forest, Scotland (Fig. 1). Pinewoods provide an interesting focus because while conservationists have been unanimous in their concern for these woodlands (Bunce and Jeffers 1977; RSPB 1993; Aldhous 1995; Mason et al. 2004), they have been more divided on the issue of how they should be managed. At the first major conference to address the ecology and management of the pinewoods, for example, some felt that the pinewoods should be regarded as relatively less disturbed than any other area of forest in the UK and that for nature conservation purposes the objective should be to encourage the forest to

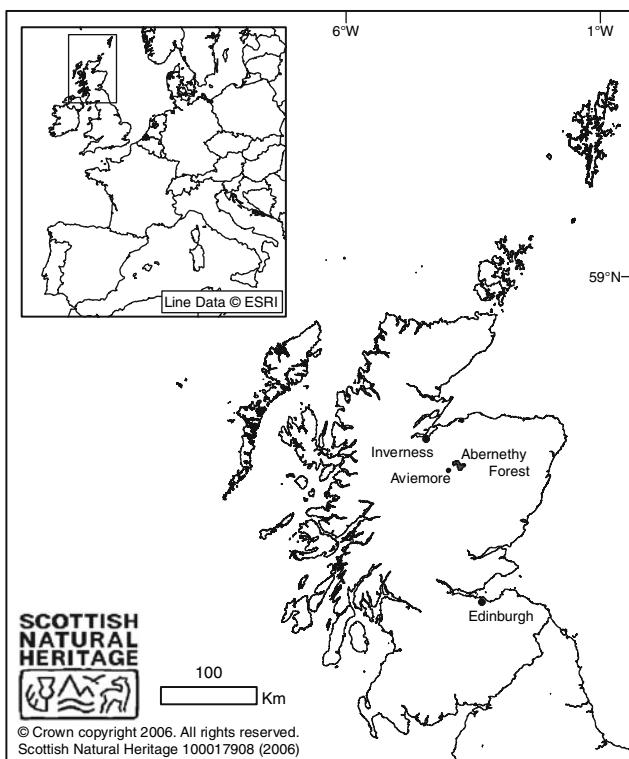


Fig. 1 Location of Abernethy forest

develop with a minimum of interference (Forster and Morris 1977, p. 117). Others, however, felt that we should not be too fearful of human intervention and that we have the ability to intervene and restore a degraded ecosystem (Gimingham 1977, p. 3). Thus debates about the management of pinewoods have focused on issues of naturalness and the appropriate degree of human intervention.

Abernethy provides a specific focus because ideas about its appropriate management are changing (Amphlett 2003). Early ideas of management revolved around reducing the grazing pressure from red deer and generally leaving the most highly valued bits of the forest to develop ‘naturally’. It was a policy that depended upon widely accepted ideas about naturalness and the need to abstract humanity from nature in order to protect it. But gradually the ideas of how best to manage the forest have begun to change. After long and ongoing periods of debate, managers are now exploring the possibility of much more complicated management regimes that involve the targeted use of fire and cattle to achieve management ends. Managers are moving towards sophisticated intervention in pinewood ecosystems but in ways that allow them to balance that intervention with enduring ideas about naturalness. Thus there has been a gradual change in the approach to management, a change that illustrates how answers to the fundamental problems of conservation (about what is natural and the degree to which people should intervene in nature) are continually being renegotiated.

By examining the management of pinewoods at Abernethy, the paper seeks to add to the work of those who have begun to unpack some of the dominant discourses of conservation (Cronon 1995; Takacs 1996; Bocking 1997; Willems-Braun 1997; Braun 2002; Brockington 2002; Adams and Mulligan 2003; Toogood 2003). The argument of this paper is that the story of nature conservation is about more than the growth of certain organisations or the wielding of power by influential individuals as is so often implied by histories of conservation (Sheail 1976, 1998; Evans 1992; Lambert 2001; Marren 2002); it is *also* a story of how ‘nature’ comes to be seen in particular ways and how that nature is constructed and reconstructed within attempts to conserve it (Adams 2003).

Drawing upon the ideas of social constructionism, the paper starts from two key presuppositions. The first is that ‘nature’ cannot be taken for granted: nature comes to take on certain meanings in society through the ways that it is represented in cultural discourse. Nature is not simply ‘out there’, separate from society and culture; ‘nature is part of culture’ (Wilson 1992, p. 12) and comes to be understood in particular ways through social and cultural processes (Evernden 1992; Wilson 1992; Harrison and Burgess 1994; Cronon 1995; Hannigan 1995; Macnaghten and Urry 1998; Demeritt 2001). As such, we must recognise that answers to the questions about what is natural and how we should act will vary and be related to the way that nature is constructed in society. Indeed, if we accept that nature is constructed, then we must also recognise that conservationists are themselves involved in processes of constructing nature (even if they are usually unaware of doing so). As they argue that some aspects of the natural world are more special than others, and as they seek to act on behalf of some species and not others, they are constructing nature. Conservationists therefore act in the ways that they do, not only because of organisational priorities or the ideas of prominent individuals, but also because of the constructions of nature that circulate within conservation.

The second presupposition is that not only are broad cultural ideas of nature constructed, scientific knowledge of nature is also socially constructed. Such ideas

are more challenging to those in conservation because while many can accept (as almost a truism) that different people have different *ideas* of nature, they invariably bracket off this area of cultural concern from the solid ground offered by science. Nature conservation, entwined as it is with the science of ecology, is surely based upon objective, rather than value-laden, understandings of nature. But if a constructivist position is taken seriously, recourse to science in this way is difficult because the focus on the constitutive nature of discourse has been extended to, and indeed took some of its impetus from, analyses of how knowledge, including scientific knowledge, is itself constructed. As Golinski puts it, ‘scientific knowledge is a human creation, made with available material and cultural resources, rather than simply the revelation of a natural order that is pre-given and independent of human action’ (Golinski 1998, p. 6; see also Knorr-Cetina 1981; Latour and Woolgar 1986; Haraway 1989, 1991; Myers 1990; Takacs 1996; Bocking 1997; Waterton 2002).

Working with these ideas, what follows examines the construction of pinewoods at Abernethy by drawing upon qualitative research involving participant observation in Abernethy’s management, an analysis of documentary material produced during the process of management and interviews conducted with site managers (Midgley 2004, unpublished thesis). An initial assessment of the issues was gained through a short-period as a volunteer engaged in practical conservation tasks. This was followed by a detailed reading of the documents concerning Abernethy’s management (management plans, research reports, articles in magazines, minutes of meetings, letters and internal position papers) and a series of semi-structured interviews with site staff that were specifically selected because of their involvement in debates about management.

The first section draws upon this qualitative material to examine the construction of the pinewoods that underpinned the initial policy of minimum intervention. The paper then looks at how the pinewoods were reconstructed when they did not respond as expected and at how management options involve balancing the desire for naturalness with the need to act for individual species. It then draws attention to the continued negotiation involved as different actors argue for different management strategies and to a discursive compromise that allows actors with diverse views to support a new management regime. The paper closes by suggesting that a recognition of the cultures of nature in conservation is important because it draws attention to parts of conservation that tend to be ignored. As conservationists focus on developing sophisticated management solutions to the problems of nature, the more fundamental ideas that underpin our actions tend to go unexamined. The paper suggests that critical reflection on the social constructions of nature that become embedded in policy is crucial if conservationists are to develop robust policies.

The early management of Abernethy

The Royal Society for the Protection of Birds (RSPB) acquired the Forest Lodge estate in 1988. This acquisition was crucial in joining together several RSPB landholdings to create the contiguous Abernethy Forest Reserve, covering close to 15,000 ha. By safeguarding the site the RSPB thought that it could make a significant contribution to the conservation of many pinewood species, but interwoven with this focus on protecting threatened species was a concern with naturalness and natural character. An influential report that helped shape the way the pinewood was

understood in the early days captured this concern: '[t]he first priority, for aesthetic, scientific and practical reasons, should be the maintenance of the naturalness of the forest' (Conservation Course 1988, p. VI). Indeed, the first management plan, written in 1991, emphasised naturalness: 'the primary management objectives should take into account the 'naturalness' of the site, and therefore follow as far as possible a non-intervention approach' (RSPB 1991, p. 38). The goal of early management was to 'reduce grazing pressures on the pinewood by ... lowering the deer population to levels where conditions will be suitable for natural regeneration' and to 'leave the native pinewood ... sylviculturally unmanaged' (RSPB 1991, p. 36). Rather than determine the shape and form of the pinewood by planting new trees, the approach adopted was to allow 'the forest to recover from past exploitation and overgrazing and to regenerate and expand where it will' (RSPB 1991, p. 38). While it was recognised that protection is itself a form of human influence and intervention, the managers sought to protect the site's naturalness by minimising intensive human influence (such as planting and harvesting) and allowing the forest to regenerate 'naturally'.

At a general level, then, the policy was straightforward. Abernethy was constructed as relatively natural and this naturalness was translated into a policy of minimum intervention. Nature was protected by removing the influence of people.

This construction of Abernethy's naturalness was, however, complicated by the simultaneous construction of Abernethy as unnatural. Ian Prestt (1988, p. 3) captured this ambiguity: '[a]t Abernethy the RSPB has secured the future of the largest remaining fragment of the ancient Forest of Caledon which once adorned the glen sides of the Scottish Highlands. In the last 500 years 99% of the once-great forest has been destroyed—and with it has gone much of its special wildlife'. The pinewoods at Abernethy are natural to the extent that they have a connection with the original, but unnatural to the extent that they have been reduced to such a small fragment. The acquisition of Abernethy was therefore thought to give 'the RSPB its best chance ever of returning an area to a near-natural condition' (Conservation Course 1988, p. 1). Similarly, an early vegetation survey suggested that '[m]anagement should be geared to restoring as great a degree of naturalness as is possible, by retaining the existing natural features, whilst removing the past influences of man as far as possible' (Tickner 1989, p. 110). The practice of minimum intervention was, therefore, more complicated than simply abstracting human influence. How could the managers protect the site's naturalness whilst also enhancing it? One implies removing human influence and the other implies applying human agency to achieve a specific end. How were the dual imperatives of *protecting* and *enhancing* the pinewoods to be balanced?

The answers that the managers found to these questions are captured succinctly by one of my interviewees:

Interviewee: ...the ethos in the late 1980s, early 1990s...was, not hands off, we were doing a lot of deer stalking et cetera, but the ethos was doing broad-brush management; when you get the principles right, other things take care of themselves...

Andrew: can you clarify, your broad brush is...

Interviewee: Our broad-brush management aims for the site are...erm aiming to expand the forest area up to the potential natural treeline. To do that

entirely or primarily through the reduction of grazing, which mainly means deer on this site. That the semi-natural woodland, the core of the old forest, will be sylviculturally unmanaged, or near as damn it... And that we have managed and re-structured our less natural plantations to push them towards more semi-natural types of woodland. So big broad-brush management aims.

Minimum intervention therefore involved culling the deer population, leaving the ancient semi-natural forest unmanaged, thinning pine plantations so as to avoid canopy closure and significant alteration of the ground flora, and removing exotic species.

As such, the managers negotiated the ambiguity of Abernethy's (lack of) naturalness in two principal ways. The first involved translating histories of human influence into a spatially differentiated management strategy. The ancient semi-natural woodlands (ASNW), pine plantations and exotic plantations were constructed, and ultimately treated, in different ways. If we conceive of a spectrum of naturalness and artificiality, the native pinewoods were constructed as remnants of naturalness and positioned near the natural end of the spectrum (Fig. 2a). Scots pine plantations, as woodlands of human origin, were considered more artificial, but viewed relatively favourably because they were understood to have the potential to take on natural qualities and to provide habitats for pinewood species. Exotic plantations were considered highly artificial: they were created by people and constituted of 'alien species'.

The policy that was developed—of leaving the ancient semi-natural forest alone, restructuring the pine plantations and removing exotic plantations—was derived from the conflation of a spectrum of naturalness and artificiality with a 'management gradient' (Fig. 2b). Instead of putting artificiality in opposition to naturalness, the Conservation Course counter-posed naturalness and intervention. The closer one is to the natural end of the gradient, the less intervention there should be. Conversely, the closer one is to the artificial end of the spectrum the more intervention there could be. Thus the managers found a way of negotiating the ambiguity of Abernethy's naturalness: the existing naturalness of the site could be protected by not interfering in the ancient semi-natural forest and the naturalness of the whole site could be enhanced by either altering or removing the artificial elements depending on their degree of artificiality.¹

The second way that managers negotiated the ambiguity of Abernethy's naturalness was through the policy of achieving natural regeneration by reducing deer numbers rather than excluding deer with the use of fences. Although 'it is pretty interventionist reducing deer densities by two thirds' (interviewee), killing hundreds of deer was compatible with a minimum intervention policy because of the perceived artificiality of the alternative, because of the way that the forest was constructed as

¹ The ambiguity of the term 'naturalness' is apparent here. On the one hand, the naturalness of the ancient semi-natural areas of forest is protected by not intervening, but, on the other hand, the naturalness of the whole forest is enhanced by intervening. In this case, the semi-natural areas are understood to be relatively undisturbed and so relatively natural in the untouched sense; intervention would be seen as detrimental. At the same time, however, the naturalness of the whole forest can be enhanced by altering plantations and removing exotic species because naturalness in this context refers to *natural character*. The managers want to intervene to shape the pinewood so that it achieves a set of characteristics that would be apparent in a natural forest in the untouched sense. Thus the ambiguity of the term 'naturalness' gives rise to the apparently paradoxical situation where intervention is seen as harming nature in some situations but enhancing it in others.

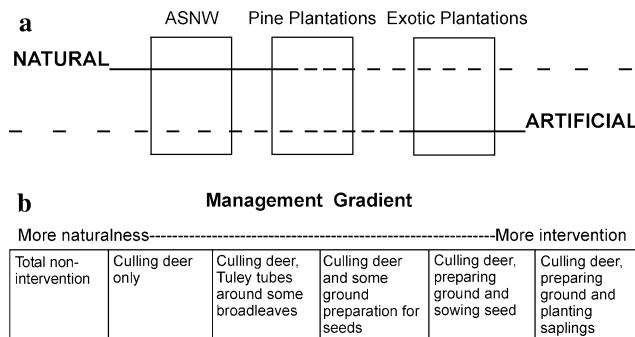


Fig. 2 **a** Positioning Abernethy on a scale of naturalness. **b** Naturalness/management gradient (Source: Conservation Course 1988, p. 22)

subject to unnaturally high-deer numbers and because culling could be represented as replicating natural processes.

While there was abundant tree regeneration at Abernethy, the full development of the regenerating trees was prevented by a high-grazing pressure predominantly from red deer (Conservation Course 1988; RSPB 1991; Taylor 1995). The key question was, therefore, how to deal with too many deer. The conventional answer, on the part of conservationists seeking to protect woodland, was to exclude the deer by building a fence around the woodland. When Abernethy was acquired, however, the use of fences in the conservation of woodlands was increasingly seen as problematic. In the context of the concern for naturalness, fences were human artefacts that would compromise the naturalness of the site both in terms of putting a manufactured object in the woodlands and in terms of rendering the forest into an artefact of management: the forest would develop without the influence of grazing and thus take on ‘unnatural’ characteristics. If the goal was woodland conservation, then deer could not simply be excluded because they were increasingly understood to play an important role in forest development: deer should be present in woodlands but in numbers that allowed forest regeneration. The use of fences, then, was understood to produce artificial results and thus to be unsuitable in a site where naturalness was a primary concern. Reducing the deer population was the only other alternative.

Such drastic intervention depended upon two arguments. The first revolved around the construction of unnaturally high-deer numbers. Steven and Carlisle (1959, p. 79) illustrated this way of seeing the pinewoods when they said that ‘[m]ost of the native pinewoods have been at one time or another part of a sporting estate in which the deer were encouraged and protected for shooting, and this has often given rise to abnormally high populations within the woodlands’. The pinewoods, whilst being remnants of natural woodland, are thus subject to excessive levels of grazing, that prevent their regeneration and compromise their naturalness. Reducing deer numbers, then, is to enhance the forest’s naturalness. It is to remove an unnatural pressure and restore the pinewood to health.

The second argument revolved around the idea of replication. The Conservation Course, for example, preferred culling to other forms of management on the grounds that culling would replicate lost elements of a natural pinewood: ‘[o]f all the alternative ways of enhancing successful regeneration—fencing, burning, screefing and

culling—we recommend culling. We justify this as part of a management strategy that stresses naturalness, by referring to the observation that, in the natural forest, deer would have to be regulated by wolves' (Conservation Course 1988, p. 57). Under such thinking, deer numbers are unnaturally high, not only because of past management practice, but because of the lack of natural predators. As such, culling is a necessary element of management. In becoming the surrogate wolf, the manager moves the system back towards a more natural arrangement. Culling is understood as a means of achieving natural balance, a situation where deer numbers are in harmony with a healthy and regenerating forest.

Ultimately, then, the managers at Abernethy in the late 1980s and early 1990s developed a management strategy that allowed them to negotiate the ambiguity of Abernethy being valued for its relative naturalness whilst also being understood as far from pristine. The emphasis was on minimum intervention. But as the fortunes of different species and habitats changed, and as policies began to have material consequences, the appropriateness of this early management regime came up for debate.

Reconstructing pinewood management

Through the 1990s the site managers got on with the business of encouraging the expansion of the woodland and enhancing the site's natural qualities by culling the deer, thinning plantations and leaving the semi-natural areas of forest untouched. By the late 1990s, however, it was becoming obvious that the expected outcomes of their policy were not materialising. With reference to their repeated surveys of regeneration, the managers could see:

...it was quite obvious that a lot happened in the first few years, but we are pretty certain that now, the rate of recruitment of new regeneration, which is a primary aim of the site, has slowed down. Deer are still in quite low numbers, probably even gone down a bit further. But we are not actually getting, rather simplistic you know, the delivery of new trees. So that was one of the first things that alerted to us that there may be a bit more to managing pinewoods than reducing deer.

Working from the idea of the semi-natural areas as remnants of naturalness subject to overgrazing—and from the idea that natural systems were relatively stable—it was presumed that if the deer were culled the forests would flourish and that naturalness would be protected/enhanced. But as the deer were being culled, woodland expansion actually appeared to be slowing down. The lighter grazing regime allowed the field layer to grow until it ultimately began to inhibit the regeneration of forest trees. The site managers therefore began to acknowledge that the policy of minimum intervention was potentially acting *against* their broad objectives of woodland expansion.

This acknowledgement prompted a prolonged period of critical reflection on policy and ideas. Since minimum intervention and the associated ideas of pinewoods were apparently taking them in the wrong direction, the managers needed to find a new direction for management and thus had to re-ask an old question: what is a natural pinewood?

To answer this question the managers could call upon different discursive resources. The first of these was the so-called 'new ecology' (Botkin 1990). Until the

1970s, ecology had been dominated by the ‘equilibrium paradigm’; ecosystems were understood to be relatively stable and predictable and, as such, could be manipulated by the ecologist or manager. Since the 1970s, however, the ideas of equilibrium, stability and the ‘balance of nature’ have been challenged. The new ecology has emphasised the non-linearity of ecological processes and the role of disturbance in ecological systems. A key point of discussion in management planning meetings at Abernethy was, therefore, the need for disturbance. An internal report that reviewed the literature on the role of fire in forest systems, for example, adopted an explicitly argumentative tone:

Climax communities were once considered to be the most stable in terms of structure, species diversity, fertility and in nutrient production, retention and recycling. Any large-scale disturbance was seen as a ‘backward step’ as it stopped the forest reaching the climax stage... The reverse is now seen to be true. Climax communities are not stable because fire and windthrow initiate successional changes in the community...climax forests are probably rare (Proctor 1998, p. 11, unpublished report).

Ecological theories are themselves claims to define the nature of natural woodland and debates in academic ecology were called upon and used as argumentative resources by those that wished to argue for different forms of management.

A second set of discursive resources called upon to reconstruct the natural pinewood were historical. Although the human history of the forest was well known when the RSPB took on the Forest Lodge estate in 1988 (O’Sullivan 1973; Munro 1988), this history was played down (Conservation Course 1988; RSPB 1991). The semi-natural forest was understood to have remained relatively intact and retained considerable natural qualities despite past exploitation. Indeed, it was this emphasis on their relative naturalness that led to the policy of leaving these areas silviculturally unmanaged. But as the policy of minimum intervention was being rethought, the history of the forest was brought back to the foreground. The following interviewee, for example, questioned the notion that the semi-natural areas could provide a model forest towards which to aim. Comparing the widely spaced, broad crown trees of the semi-natural areas with the tall straight trees that were regenerating he asked:

Interviewee: how come natural regeneration doesn’t look like the stuff that we have got now...?

Andrew: what do you mean by the stuff we have got now?

Interviewee: er well these kind of big broad Granny pines ... those big trees is what I class as the stuff we have got now and looking at the historical evidence ... those big trees are the result of what humans did 200, 300 years ago. The natural regeneration doesn’t look like that, they are tall, straight, quite a small canopy, erm more branches have dropped off naturally, so the form is not the same. That is not to say that you won’t get ... these big broad canopy pines in a natural forest, you will get them, but probably rarer.

By bringing the history of the forest to the foreground, a different idea of the natural forest began to emerge. Since the past management of taking trees for ships’ masts has resulted in the spaced character of the forest, a forest that has not had such selective human management would be naturally more dense. A natural forest

would be made up of relatively straight, tall trees. Thus as managers discussed management they were reconstructing the pinewoods and ideas of what pinewoods should be like.

The pinewoods were, therefore, being reconstructed. A new idea of what they should be like was emerging. But as a new set of attributes and processes came to be understood as necessary to pinewoods, questions were asked about the degree to which management should work towards restoring those attributes and processes. Should broadleaf species be encouraged? Should fires be left to burn? How can lost processes of disturbance be replicated? These questions returned the managers to the issue of intervention, an issue that remained contested.

For some, even though they recognised that minimum intervention had negative effects, and that the forest had a long history of human influence, minimum intervention was still the way forward:

Andrew: ...I just wondered where you stood on naturalness and intervention in the forest. How far should we be intervening?

Interviewee: I would probably put myself in the non-intervention camp. So maybe not pure sort of non-intervention as such, probably minimalist. So we obviously, we are keeping tracks open, so I would say if a tree falls across a track you would maybe cut the centre out of the tree, take that centre up and throw it to the side. So you are not taking anything off the site but with the tracks are still usable or for health and safety reasons you might have to cut something down, but other than that I would say...very, very little human intervention.

This interviewee disliked the thought of intervening because of what he saw as the arbitrary nature of management goals. He wanted to 'let the forest go' and just live with the consequences. If the result turned out to be a downturn in species numbers, he would argue that we should just wait and instead of judging the forest in a human timescale we should allow the forest time to develop and take on its own natural character.

For others, though, continuing with the policy of minimal intervention was not an option. The following interviewee was much happier to get on with the business of managing the forest to achieve specified goals. Since the forest was already the product of past management it was not 'natural' and thus not necessarily damaged by further human management:

I'm definitely in the camp: what we've got is not natural, we should be managing it for what we want to manage it for and we shouldn't be ashamed of saying that. ...I think generally speaking it's a cultural landscape and if we want to have lots of capercaillie I think we know how to do that. We shouldn't be ashamed of saying we are managing this reserve for these birds and creating a natural forest is a secondary aim because its almost an impossible thing to do isn't it, re-creating a native woodland.

The reassessment of the policy of minimal intervention in management planning meetings through the late 1990s opened up, therefore, a complex arena of negotiation. As the constitution of a natural pinewood was discussed, questions of objectives were raised, and as objectives verged into issues of intervention and naturalness, so broad argumentative positions on appropriate management developed.

Towards a resolution

Debate about appropriate management did not, however, simply centre on issues to do with intervention and the definition of what was ‘natural’ and ‘artificial’. At the same time, species such as the capercaillie *Tetrao urogallus* were declining drastically. Reflecting on some of the subtle changes in emphasis at Abernethy, one member of staff suggested that ‘all along, consistently for all the management plans, the primary objective was the expansion of the woodlands by regeneration...there is no debate on that’. But he went on to say that:

In more recent years probably from about 1995, 1996 you will see that individual species requirements, particularly key birds like capercaillie and black grouse have a far higher profile...they are far higher up the profile now because they have declined. You know, since the last national survey there has been a 50% decline of capercaillie in the last 8 or 10 years. So the requirements of these key species is higher up on our agenda than it was ten years ago.

The long-term objectives of developing a forest of natural character had to be balanced with the short-term imperative to act for the capercaillie. Crucially, though, questions of what to do to save the capercaillie coincided with questions about pinewood management more generally. While capercaillie are thought to require a mosaic of heather *Calluna vulgaris* and blaeberry *Vaccinium myrtillus* for feeding and breeding, a review of capercaillie research highlighted that:

excluding deer by fencing or by reducing densities through culling results in the vegetation becoming increasingly long and dominated by heather. In addition to the loss of blaeberry, young chicks appear to find it difficult to manoeuvre in such tall vegetation (Petty 2000, np).

The situation in Abernethy, with its long heather, resulting from high rates of culling, was, in addition to limiting regeneration, potentially causing problems for the capercaillie. With this situation in mind, Petty suggests that:

Consideration needs to be given to how the ground vegetation can be better managed in these stands, including management options that will increase nutrient cycling and in so doing lead to a revival of blaeberry and provide better access and foraging for broods (Petty 2000, np).

Minimum intervention was again challenged. If nature was left to take its course, the pinewood field layer could develop in ways detrimental to the capercaillie. Thus those that preferred a policy of minimal intervention were fighting a losing battle. As concerns for the capercaillie coincided with concerns about regeneration, the discussion turned from abstract arguments about intervention towards discussions about what intervention could be undertaken. Managers began to consider their options for managing the field layer.

Informed by the new ecology and its emphasis on disturbance processes such as fire, storms, disease and grazing, the managers asked whether these processes could be encouraged at Abernethy. The answer was no. Concern with natural processes and natural forests had to be negotiated with reference to the specific situation at Abernethy which was seen as a small fragment of forest that could be damaged by unrestrained natural processes such as fire. It was argued that fires could easily destroy the majority of the forest that was valued the most. Thus whilst disturbance

was needed for the perpetuation of the woods, too much disturbance would potentially ‘be detrimental to the site and resource of this habitat in Scotland’ (Anon. 1998, unpublished report). If a natural fire started, it would still be put out because of the risk to the forest. The managers were left in a position of accepting the need for disturbance but not being able to allow it if it occurred because of the potential harm that it would do to the forest. It was an apparent impasse that was overcome by developing the notion of ‘controlled disturbance’. The managers began to consider being able to not only control unwanted disturbance, but also to be in control of where, when and to what end disturbance occurred. They began to explore the possibility of strictly controlled burning in the forest, tractor mounted swiping of the field layer and cattle grazing.

But whilst it looked like those in favour of intervention had won out, it is not the case that the concept of naturalness was discarded. The particular forms of management that were proposed represented a compromise that attempted to balance intervention with naturalness and management for the capercaillie with management for regeneration. Even as managers drew upon ideas from the new ecology and discussed ways of replicating disturbance, the actual forms of intervention considered represented an accommodation with issues of naturalness:

I don’t have a problem with intervention, provided we always have this in our mind that we intervene using as near natural prescriptions as possible. For example, we get the cattle in to do a job as a surrogate for the reindeer or the elk or whatever would have done that job in the past...We might create a seed bed by burning or having cattle in but we probably wouldn’t dream of having a JCB in to create a seed bed because that is certainly not natural whereas the burning and the cattle are mimicking natural processes.

The sorts of management being considered thus represented a compromise that was acceptable to both those that would prefer less intervention and those that were relatively happy with intervention. Management by fire or controlled grazing (options understood to replicate disturbance processes in a natural forest) was acceptable to those who were sceptical about the need for human intervention because such management was understood to be more ‘natural’. Instead of coming into conflict, the relatively interventionist species management coincided with habitat management. The worries of some that managing for the capercaillie would result in the pinewood turning into an artificial capercaillie factory were potentially allayed because the sorts of management that could be undertaken could, at the same time, be understood as replicating natural processes and thus working towards natural character.

Ideas therefore began to coalesce around a new potential management regime. But changing management is a long-process and established practice could not simply be altered. Managers did not know, for example, whether a new form of management based around their ideas of disturbance and the practices of controlled grazing and burning would produce the desired effects. Consequently, they turned to research and began designing projects that would allow them to see if burning produced the conditions for forest regeneration they desired or altered the field layer in ways suitable for capercaillie. Ultimately, this research (see Hancock et al. 2005, p. 210) suggests that a move towards more intervention through controlled burning is likely, but as the contestation of this account suggests, such a strategy is likely to be the focus of continued debate.

Conclusion

The management of pinewoods at Abernethy is, as this narrative has demonstrated, changing. The initial approach of minimum intervention was underpinned by ideas of the pinewood as relatively natural and existing in a state of perturbed equilibrium. But as those ideas were made real and had material effects, the forest itself changed. A uniformly deep field layer with long heather and thick mosses developed and the expected forest regeneration did not materialise. The changing nature of the forest therefore prompted critical reflection upon prior ideas and policy. In a subsequent period of debate and negotiation the managers began to re-imagine the forest. Utilising a broad range of discursive resources, the managers debated the nature of a natural pinewood and the extent to which such woodland could be restored. In the process, different managers and researchers took up contrasting argumentative positions on issues to do with the appropriate degree of intervention, the extent to which management should focus on one species and the degree to which new ideas in ecology could be applied. As ideas coalesced around a new image of the forest as in a continual process of change and disturbance, the managers started to explore the potential ways of replicating disturbance or controlling it with ‘natural management tools’. These ‘tools’—such as fire and cattle—provided a means of achieving controlled disturbance, but also, at the same time, a means of finding an accommodation between those who wanted to restrict, and those that were happy to pursue, intervention. Ultimately, research was conducted into the effects of controlled disturbance and the positive results move the pinewood managers one step closer to much more complex management regimes.

What I have sought to emphasise in this narrative of changing ideas about management is that the nature that is being conserved is the product of cultural politics. As the minimum interventionist policy was questioned, for example, the very idea of the ‘natural’ pinewood was itself questioned. New discursive resources were called upon to reconstruct the natural pinewood in order to rework management options. The pinewoods that were understood as being relatively stable came to be understood as actually subject to instability and disturbance. Thus the very idea of a natural pinewood was revised. What was natural had changed. The natural pinewood emerged in the development of attempts to conserve it. While there is a real world of plants and animals beyond the human imagination, ‘nature’ and ‘pinewoods’ as human categories and constructs, are embedded in, and emerge through, cultural politics.

Pinewood conservation must, therefore, be understood as a culturally and socially negotiated achievement. In contrast to the conventional view of conservation that sees it as applied ecology and thus an arena of science that lies outside the messy world of cultural negotiation, this story draws attention to the construction of nature and the negotiation of argumentative positions within conservation itself. Minimal intervention as a policy, for example, depended upon the construction of the pinewoods’ naturalness and their connection with a pre-human pristine nature. More recently, as this policy has been questioned, the pinewoods have been reconstructed through ideas of their departure from naturalness and their history of human management. Managers have drawn upon discursive resources from the ‘new ecology’ and environmental history to reconstruct the forest and to work towards new management regimes. As such, the story of the development of pinewood conservation

cannot simply be understood through recourse to the importance of key individuals or organisations (as is often the case in histories of conservation): it also has to be understood as a cultural process within which particular ways of seeing nature are contested, negotiated and made real.

Instead of viewing changes in policy as simply the outcome of the gradual triumph of science and the development of ‘better’ knowledge, the approach taken here allows us to see a much more messy and political process. While shifts in management at Abernethy could be understood as a straightforward response to the failings of minimum intervention—the policy was not working, so it was changed and based upon better ecological knowledge—such a reading would overlook the fact that the ability of managers to see one course of action as ‘appropriate’ and another as ‘inappropriate’ involves a great deal of discursive and interpretative work and that the very idea of what is being conserved, changes. Current policy is not simply a response to the failings of prior policies because a great deal of discursive work goes into the development of policy and there is a continuing process of discursive contestation through which policies are constantly reviewed.

Such an understanding has important consequences for conservation. If it is accepted that cultures of nature become embedded in conservation policy, it is vital that they are recognised and critically reflected upon if conservation is to move forward in a productive way. An awareness of the way that nature is constructed should be central to developing initiatives within conservation.

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Identifying new buffer areas for conserving waterbirds in the Mediterranean basin: the importance of the rice fields in Extremadura, Spain

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Abstract The impact of wetland loss on migratory waterbirds can be mitigated by the presence of anthropogenic habitats such as rice fields. In the Mediterranean basin, wetlands have been drained and altered to such a degree that their very existence is threatened. It is, therefore, essential to identify key buffer areas in the basin to develop conservation strategies for migratory waterbirds. In Extremadura, continental SW Spain, 30,000 ha of new rice fields have created since the 1960s. The present study describes for the first time the waterbird community associated with these inland rice fields, and addresses the question of the potential value of this area in buffering the loss of natural wetlands for populations of waterbirds using the East Atlantic Flyway (EAF). The waterbird community studied consisted of 45 species, with population levels reaching values of international importance (>1% of the biogeographical population using EAF) for the Common Crane *Grus grus* (19%), Black-tailed Godwit *Limosa limosa* (1.2%), Black-winged Stilt *Himantopus himantopus* (1.2%), and Cattle Egret *Bubulcus ibis* (1%). The presence of these rice fields may be modifying the wintering and/or feeding sites of some waterbird species such as the Common Crane and Black-tailed Godwit. Unfortunately, there is no legal protection for this area. We propose the designation of these rice fields as a Special Protection Area for birds.

Keywords Anthropogenic habitats · Black-tailed godwit · Common crane · East atlantic flyway · Rice fields · Shorebirds · Waterbirds

Introduction

Recent reviews of the population status of long-distance migrant waterbirds show that many populations are declining worldwide. In the East Atlantic Flyway and

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Black-Sea/Mediterranean Flyway, for example, 37% and 65% of shorebirds with known population trends are declining, respectively (International Wader Study Group 2003). Although the reasons for the declines are poorly understood, the alteration or loss of natural wetlands in the flyways are probably the main cause of the declines (Morrison et al. 2001). In addition, some scenarios of the potential impact of climate change on different waterbirds show continuing declines through to the late 21st century (Rehfisch et al. 2004).

In a migratory flyway, previously unused staging and/or wintering areas can act as buffer areas against the impact of habitat loss (Weber et al. 1999). For example, Red-breasted Gees *Branta ruficollis* wintered in the Kirov Bay (Caspian Sea) until the 1960s (see Sutherland and Crockford 1993). Due to a change in agriculture from cereal and rice crops to cotton, since the early 1970s, however, the majority of the world population has moved to the Dobrega region, Romania. This previously unused wintering area buffered the loss of the traditional wintering area (Sutherland and Crockford 1993). It is thus important to identify valuable buffer wetlands that may supplement declining natural habitats in designing strategies to conserve migrating waterbirds (Elphick 2000; Masero 2003).

Agroecosystems continue to have increasing weight in determining biodiversity conservation policies, since not only do they constitute one of the world's most extensive biomes, but also new areas are constantly being developed (Elphick 2000). As part of this process, new land uses have appeared that are today beginning to be valued as buffer habitats that can support some of the communities that are under ever-greater threat (Hilton-Taylor 2000). Several studies have shown that rice fields are anthropogenic habitats that can provide suitable staging and/or wintering areas for migrating waterbirds in Europe, North America, and Asia (Fasola and Ruiz 1996; Elphick 2000, 2004; Manley et al. 2004; Maeda 2005). The main reason is that these croplands contain areas that remain flooded to a shallow depth over long periods (Brouder and Hill 1995).

About 581,978 ha of rice is harvested in Europe annually (Ferrero and Nguyen 2004). Its role in providing functional wetlands for waterbirds will vary according to the cropping regime, time of year, and geographical position in the flyways. In Extremadura, SW Spain, about 30,000 ha of inland rice fields have been created since the 1960s. The importance of these rice fields for waterbird species remains largely unknown. To date, there has been no legal protection provided for this area, and it is not listed among the main sites for waterbirds in Spain (Martí and Del Moral 2003). In the present study, we report the international importance of these rice fields for several waterbirds of special conservation interest by comparison against existing criteria. Due to the strategic geographical position of the Extremadura's rice fields on the East Atlantic Flyway (EAF), we address the question of the potential value of these anthropogenic wetlands as buffer areas against the loss of natural habitats for waterbird populations migrating between Europe and Africa.

Methods

Study area

The rice fields are located in the middle basin of the River Guadiana in Extremadura (SW Iberian Peninsula; 38° N, 6° W). As the result of transformation in land use,

especially in the 1960s and 1970s, large expanses of rice fields have been created in this basin (30,000 ha in 2004). This transformation consisted fundamentally in putting historical extensive drylands, both wooded and unwooded, under irrigation (Sánchez et al. 1993).

A low and gently undulating relief (206–426 m a.s.l.) and a predominantly siliceous geology characterize the area (Zamora 1987). The climate is typically Mediterranean (Felicísimo et al. 2001), and many dams have been constructed to regulate the hydrological system to prevent flooding and for irrigation (García 1994). There are five large reservoirs (Cíjara, Puerto Peña, Orellana, Zújar, and Serena) located in the region of the upper floodplains (named ‘Vegas Altas’), as well as others of smaller size.

The rice production cycle begins with preparation of the fields from March until mid-April, followed by flooding and sowing from the second half of April until the end of May. Germination, growth, flowering, and ripening continue through to September, and harvesting is in October and the first half of November. The final procedure carried out from then until the end of December is rolling the standing straw flat into the mud under flooded conditions, leaving large expanses of shallow water which, if the autumn rains are normal, remain throughout the winter until the cycle begins again.

Bird censuses and international importance of the waterbird populations

We considered as ‘waterbirds’ the families of birds included in the work by Rose and Scott (1997). To estimate waterbird population sizes, we performed monthly surveys of the whole study area during 1991–1995. The study area was divided into five zones (range: 4,000–7,000 ha), which were counted simultaneously to avoid errors due to bird movements between adjacent areas. We scanned each zone using binoculars and telescopes from a car (>90% of the study area can be surveyed from the roads).

Following Rose and Scott’s (1997) criteria, we considered that the study area should be considered internationally important if it regularly supports 1% of the individuals of one species or subspecies of waterbirds.

Data analyses

Ecological indices were used to provide summary information about the waterbird community associated with the rice fields. The monthly means for species richness and the total number of individuals were calculated for the whole period. These monthly values were then used to calculate the Shannon–Wiener diversity (Magurran 1989) and the Lebreton dominance (Thevenot 1982). Values of the diversity between months were compared by means of the Hutcheson test (Hutcheson 1970). The similarity between monthly censuses was calculated using the Czechanowski–Dice–Sorensen measure, and the resulting similarity matrix was used to perform a cluster analysis using the unweighted pair-group method with arithmetic averaging (UPGMA) (Sokal and Michener 1958). Trophic categories (omnivores, herbivores, and carnivores) were established on the basis of quantitative diet data in Cramp and Simmons (1977, 1980, 1983). We used a Mann–Whitney *U*-test to compare numbers of birds between periods because the normality and homoscedasticity conditions were not met.

Results

A total of 45 species belonging to 15 families were observed in the study area (Tables 1 and 2). The monthly mean population varied between 746 individuals in May and 19,195 in January. The cluster analysis showed two differentiated periods in the waterbird community's use of the rice fields: one from May to September, and the other from October to March (Fig. 1). The number of birds varied significantly between these two periods ($U_{14,10} = 26$, $P < 0.01$).

The May–September period was characterized by having the smallest populations (range: 746–3,665; Table 1), and the lowest value of the species richness observed over the course of the year (Fig. 2). There was one group of species that constituted the breeding community (e.g., Collared Pratincole *Glareola pratincola*, Black-winged Stilt *Himantopus himantopus*, Eurasian Coot *Fulica atra*, and Moorhen *Gallinula chloropus*), another group that bred in nearby zones and used the rice fields to feed (White Stork *Ciconia ciconia*, Grey Heron *Ardea cinerea*, Cattle Egret *Bubulcus ibis*, and Gull-billed Tern *Gelochelidon nilotica*), and two late migrants (Whiskered Tern *Chlidonias hybrida* and Black Tern *Chlidonias niger*). The guild that completely dominated the community is that of the insectivores and carnivores (Fig. 3). The May–September period was separated into two sub-periods: A1 and A2 (Fig. 1). The earlier, A1, was characterized by fewer birds and the presence of breeders and late migrants (Table 1). In the later, A2, the populations were larger, and feeding groups of Ardeidae and Laridae increased, with some breeders staying on (Tables 1 and 2).

The October–March period (Fig. 1) includes the migratory and wintering periods. Its main characteristic was a high species richness (Fig. 3) and consistency in families that dominated (Table 2). Three sub-periods could be distinguished: B1, B2, and B3 (Fig. 1). The first, B1, corresponded to the post-summer recuperation of the total number of individuals (Table 1), accompanied by an increase in the species richness and diversity (Fig. 2). A strong autumn migration influx led to the Charadriidae, Laridae, and Scolopacidae joining the Ardeidae as dominant families (Table 2). Despite this taxonomic shift, the community remained dominated by insectivores and carnivores (Fig. 3) until December (sub-period B2) when community came to be dominated by omnivores (mainly waterfowl) (Fig. 3). Abundance also peaked in mid-winter (Table 1), and species richness and diversity were both high (Fig. 2). The dominant groups of the previous sub-period are joined by the Common Crane *Grus grus*, which was the most numerous species in the rice fields. At the end of this period, the Anatidae populations began to dominate (Table 2). This carried over into the subperiod B3, which was characterized by a marked spring migration of Scolopacidae (Tables 1 and 2), leading to the highest values of species richness and diversity during this sub-period, and neither trophic guilds dominating the community.

The species with international importance were Common Crane (19%), Black-tailed Godwit *Limosa limosa* (1.2%), Black-winged Stilt (1.2%), and Cattle Egret (1%).

Discussion

Extremadura's rice fields clearly have a continental nature. There is no influence of coastal marshes which can condition the characteristics and structure of the

Table 1 Monthly mean number of 45 waterbird species cited in the rice fields

| Species | A1 | | A2 | | B1 | | B2 | | B3 | | |
|-------------------------------|--------|-----------|---------|---------|---------|-----------|-----------|-----------|-----------|---------|---------|
| | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 1 | 2 | 3 |
| <i>Anas acuta</i> | | | | | | 2.0 | 6.0 | 29.0 | 35.0 | 35.0 | |
| <i>Anas clypeata</i> | 1.0 | | | | | 17.0 | 208.0 | 174.0 | *257.0 | 13.0 | |
| <i>Anas crecca</i> | | | | | 1.0 | 15.0 | 11.0 | 448.7 | *312.0 | *169.0 | |
| <i>Anas penelope</i> | | | | | | 14.0 | 8.0 | 159.3 | 172.7 | 47.0 | |
| <i>Anas platyrhynchos</i> | *30.7 | 21.0 | 8.0 | 10.0 | | | | | | | |
| <i>Anas strepera</i> | | | | | | | | | | | |
| <i>Anser anser</i> | | | | | | | | | | | |
| <i>Ardea cinerea</i> | | | | | | | | | | | |
| <i>Bubulcus ibis</i> | 5.0 | **2,513.0 | **803.0 | **700.0 | 11.5 | 19.0 | 29.5 | 34.0 | 178.5 | 176.0 | 77.5 |
| <i>Egretta garcea</i> | 6.0 | **61.0 | 65.0 | 17.0 | **139.5 | *169.0 | *831.0 | **524.0 | 320.5 | 175.5 | 10.0 |
| <i>Ixobrychus minutus</i> | | | | | | 61.5 | 136.5 | 87.0 | 16.0 | 320.5 | **459.5 |
| <i>Ciconia ciconia</i> | *24.0 | **64.0 | **187.0 | 4.0 | *80 | 68.0 | *225.0 | *252.0 | 62.7 | 19.0 | **250.0 |
| <i>Plegadis falcinellus</i> | | | | | | | | | | | |
| <i>Charadrius dubius</i> | 1.5 | 1.0 | 77.0 | 3.0 | 24.0 | 16.0 | 35.0 | 1.0 | 28.0 | 22.7 | 8.0 |
| <i>Charadrius hiaticula</i> | *18 | | 1.0 | | | | | | | 1.0 | |
| <i>Pluvialis apricaria</i> | | | | | | | | | | | |
| <i>Pluvialis squatarola</i> | 1.0 | **73.0 | 45.0 | **60.5 | *57.5 | **1,567.0 | **1,568.0 | **1,083.0 | *1,247.3 | **864.3 | **972.0 |
| <i>Vanellus vanellus</i> | 10.0 | **86.3 | *26.0 | *120.0 | 12.5 | **149 | 3.0 | 14.0 | **512.0 | 46.0 | 46.0 |
| <i>Glareola pratincola</i> | | | | | | | | | | | |
| <i>Larus fuscus</i> | | | | | | | | | | | |
| <i>Larus ridibundus</i> | 15.0 | 4.0 | 46.0 | **75.5 | **450 | **1,896.0 | **3,421.0 | **2,086.0 | 740.7 | 46.0 | 46.0 |
| <i>Himantopus himantopus</i> | *198.0 | *548 | *461.5 | *53.5 | 5.0 | 5.0 | | | | | |
| <i>Recurvirostra avosetta</i> | 4.0 | | | | | | | | | | |
| <i>Actitis hypoleucos</i> | 5.0 | | 14.5 | 10.0 | 1.5 | 3.0 | 2.5 | 43.0 | 29.0 | 12.0 | 26.5 |
| <i>Calidris alpina</i> | | | | | 1.0 | 16.0 | *176.5 | 1.0 | | | |
| <i>Calidris minuta</i> | | | | | 9.0 | 22.5 | 25.0 | 192.5 | 599.0 | 1.0 | 3.0 |
| <i>Gallinago gallinago</i> | | | | | 1.0 | *50 | **466.5 | 219.0 | 621.3 | 15.0 | 25.0 |
| <i>Limosa lapponica</i> | 2.0 | 2.0 | 34.0 | 2.0 | 6.0 | 4.0 | 3.0 | **517.0 | **2,753.0 | **473.0 | 9.5 |
| <i>Limosa limosa</i> | | | | | | | | | | | |
| <i>Numenius arquata</i> | | | | | | | | | | | |
| <i>Phalaropus tricolor</i> | 2.0 | | 21.0 | | **119.5 | | *199.0 | 120.0 | 4.0 | 17.5 | 23.0 |

Table 1 continued

| Species | A1 | | A2 | | B1 | | B2 | | B3 | | |
|-------------------------------|---------|-------|---------|---------|---------|---------|---------|----------|----------|---------|---------|
| | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 1 | 2 | 3 |
| <i>Tringa erythropus</i> | *18.0 | | | | 16.0 | | | | 2.5 | 16.0 | 8.0 |
| <i>Tringa nebularia</i> | 4.0 | | 4.0 | | 15.0 | 32.0 | 10.0 | 13.0 | 31.5 | 4.5 | 1.0 |
| <i>Tringa ochropus</i> | 3.0 | 3.0 | 24.0 | 12.0 | 3.5 | 52.0 | 23.0 | 10.0 | 21.5 | 11.0 | 17.0 |
| <i>Tringa totanus</i> | 1.5 | | 2.0 | 3.0 | 26.5 | 38.0 | 46.0 | 16.0 | 23.0 | 61.0 | *161.0 |
| <i>Chlidonias hybrida</i> | *18.0 | | | | | | | | | | |
| <i>Chlidonias niger</i> | *22.0 | | | | | | | | | | |
| <i>Gelochelidon nilotica</i> | 6.0 | | 24.5 | 3.0 | | | | | | | |
| <i>Sterna albifrons</i> | 2.0 | 1.0 | 1.0 | 9.0 | 2.0 | | | | | | |
| <i>Circus aeruginosus</i> | | 4.0 | | | | | | | | | |
| <i>Pandion haliaetus</i> | | | | | | | | | | | |
| <i>Grus grus</i> | | | | | | | | | | | |
| <i>Fulica atra</i> | **101.0 | | | | | | | | | | |
| <i>Gallinula chloropus</i> | **205.0 | 8.0 | 18.5 | | 18.5 | | | | | | |
| <i>Tachybaptus ruficollis</i> | | | 7.0 | | | | | | | | |
| <i>Total individuals</i> | 746.0 | 994.0 | 3,665.5 | 1,099.5 | 1,877.5 | 4,288.0 | 7,569.5 | 10,943.0 | 19,195.0 | 8,781.8 | 4,361.0 |
| <i>Total species</i> | 23 | 14 | 22 | 19 | 22 | 18 | 27 | 29 | 32 | 33 | 28 |

Letters (A–B) and numbers (1–12) in the first row is the cluster analysis assignment of months

Lebreton dominance index: * subdominant; ** dominant

Table 2 Monthly mean abundance of 15 families cited in the rice fields

| Family | A1 | | A2 | | B1 | | B2 | | B3 | |
|--------------------------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|
| | | | | | | | | | | |
| | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 1 | 2 |
| <i>Anatidae</i> | *4.1 | 2.2 | 0.2 | 0.9 | 0.1 | 0.0 | 0.7 | *3.7 | **5.5 | **10.5 |
| <i>Ardeidae</i> | 1.5 | **6.1 | **70.5 | **74.9 | **45.4 | **5.8 | **13.2 | **6.0 | 1.9 | **5.8 |
| <i>Ciconiidae</i> | *3.2 | **6.4 | **5.1 | 0.4 | *4.3 | 1.6 | *3.0 | *2.3 | 0.3 | **6.7 |
| <i>Threskiornithidae</i> | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 1.4 |
| <i>Charadriidae</i> | *4.1 | *7.5 | *3.4 | **5.8 | *4.3 | *36.9 | *21.3 | *10.4 | *7.2 | **25.3 |
| <i>Glaucidae</i> | *11.6 | *2.6 | *3.3 | 1.1 | **7.9 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| <i>Laridae</i> | 2.0 | 0.4 | 1.3 | **6.9 | **24.1 | **44.5 | **48.9 | **24.2 | *4.2 | **16.6 |
| <i>Recurvirostridae</i> | **27.1 | **55.2 | **12.6 | **4.9 | 0.3 | 0.1 | 0.0 | 0.4 | 0.2 | 0.3 |
| <i>Scolopacidae</i> | **4.8 | 0.5 | *2.7 | *2.5 | **13.2 | *10.5 | *12.6 | *10.5 | *22.0 | **45.4 |
| <i>Sternidae</i> | **6.2 | 0.2 | 0.7 | 0.3 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| <i>Gruidae</i> | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.6 | **44.0 | **62.0 | **5.1 |
| <i>Rallidae</i> | **35.5 | **18.9 | 0.2 | 1.7 | 0.0 | 0.4 | 0.0 | 0.3 | 0.2 | 0.3 |
| <i>Podicipedidae</i> | 0.0 | 0.0 | 0.0 | 0.6 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |

Letters (A–B) and numbers (1–12) in the first row is the cluster analysis assignment of months

Fig. 1 Similarity between mean monthly numbers. Cluster analysis (UPGMA) using the Czechanowski index

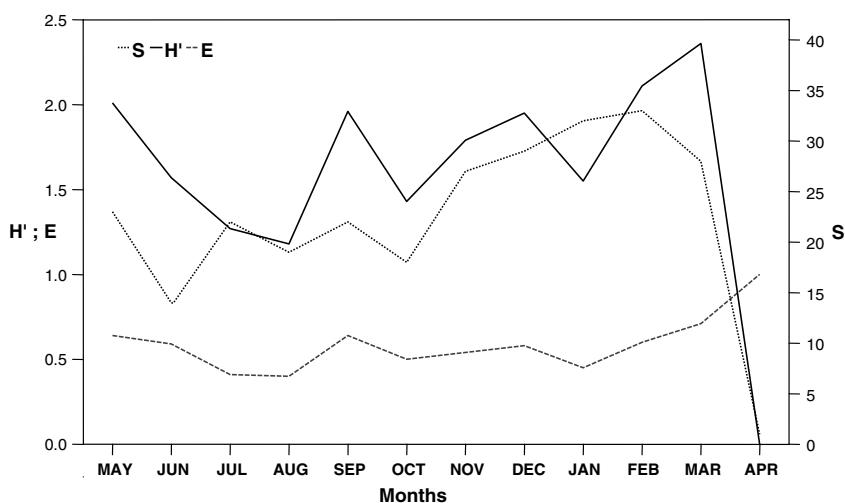
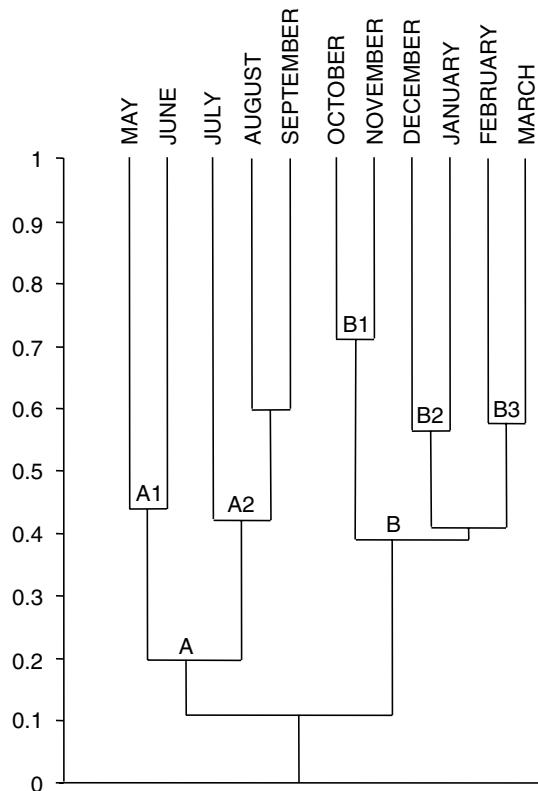


Fig. 2 Monthly distribution of mean diversity and similarity measures (S : total number of species in the community; H : Shannon's diversity index; E : equitability)

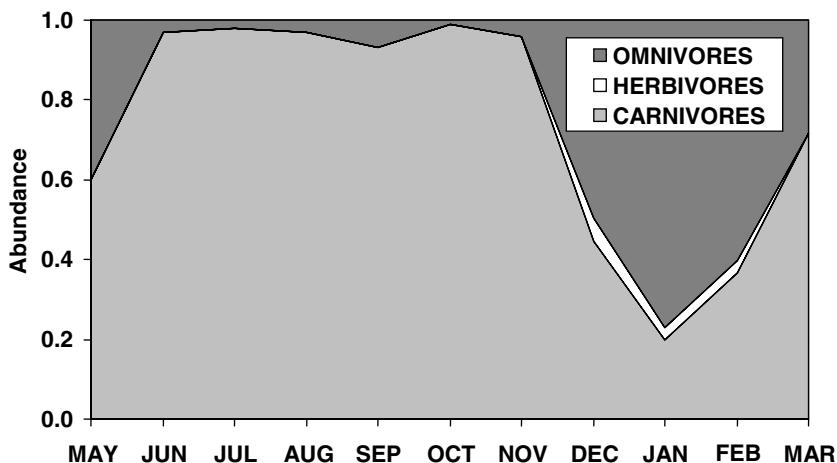


Fig. 3 Evolution of trophic groups during an annual cycle

waterbird community, as is the case in most rice-growing areas of the Mediterranean basin (Fasola and Ruiz 1996; Fasola et al. 1996; Tourenq et al. 2001). Unlike many other situations (Fasola and Ruiz 1996; Fasola et al. 1996; Elphick and Oring 1998, 2003; Shuford et al 1998; Tourenq et al. 2001, 2003), the Extremadura's rice fields did not result from the direct transformation of natural wetlands. The structure of the waterbird community is therefore not a reflection of how well these species are able to withstand alterations of their habitats, but rather of their plasticity in exploiting alternative habitats in new regions.

Most of the rice fields remain flooded 'naturally' during winter, since the autumn rains maintain the saturation of the soil without any further contribution from irrigation canals, and hence without economic cost. In California, rolling and artificial flooding of rice fields has been found to significantly increase the number of species of conservation interest, the species richness, and waterbird population densities (Elphick and Oring 1998, 2003). This result also seems to be the case in our study area, since the rolling of the naturally flooded fields was found to coincide with the beginning of the increase in the number of species and individuals, and the number of birds using the zones with standing straw appeared to be very limited.

The presence of population sizes of international interest endows these inland rice fields with great importance as wintering and/or staging areas for several migratory waterbirds. In the case of migrating species, our estimates of population sizes are conservative. Unfortunately, we have no data on the turnover rate of birds passing through the study area, but the total bird number using this area during late winter is presumably greater than the number counted on any 1 day.

The creation of these rice fields could be modifying the wintering and/or feeding sites of some waterbirds using the EAF. The following examples show that this is indeed likely. Originally, most Common Cranes wintered to the south of the Strait of Gibraltar (Bedi 1926; Heim de Balzac and Mayaud 1962). However, the core of our study area later became the species' main wintering ground (Fernández-Cruz 1981; Sánchez et al. 1993), to the point that the average size of the population wintering in the zone in the period 1985–1995 surpassed 20% of the population using the flyway (Sánchez et al. 1998). This change was principally caused by

agricultural intensification, specifically by the use of rice fields as roosts during spring (Sánchez et al. 1999). There seem to be two direct causes of why the species is only observed in the rice fields from December onwards. One is that, during early winter, cranes prefer to feed on acorns and invertebrates in feeding areas other than rice fields (Soriguer and Herrera 1978; Reinecke and Krapu 1986), possibly because of the greater energy yield and the need for protein intake (Baldassarre et al. 1983; Reinecke and Krapu 1986). The other is that the rice-straw rolling following harvest does not usually begin until November, so that access to unharvested grain is greatly hindered before then by the standing stubble (Genard et al. 1991; Sánchez et al. 1993). Furthermore, at the end of this period, spring roosting and feeding both take place in these rice fields. There would thus be a consequent major saving in energy from not making the long (of the order of 100 km) flights to and from the area's reservoirs, and this would favour the preparation for the beginning of migration (Sánchez et al. 1999).

In the case of the Black-tailed Godwit, the birds observed would be mainly *Limosa limosa limosa*, since this subspecies is of more regular occurrence in continental wetlands (Beintema and Drost 1986). This subspecies seems to have undergone some changes in its spring migratory pattern, spending more time in Africa and then flying more directly and rapidly across Europe to its breeding sites (Beintema and Drost 1986). Our results, however, run contrary to this apparent change for a significant percentage of the population using the EAF, since large contingents of birds were observed from January through to March. This might indicate that inland areas of the Iberian Peninsula, which generally are not prospected even though they are well suited to supporting migrating populations, are being used as refuelling areas. The geographical situation of the Extremadura rice fields would allow migrants to cross the interior of the Iberian Peninsula instead of following the coastal route, which was the pattern deduced from ringed-bird recoveries in past decades (Beintema and Drost 1986). Lastly, it must be noted that some recent non-systematic counts in the rice fields (up to 9,026 birds; Martí and Del Moral 2003) suggest that the number of Black-tailed Godwits migrating through the study area is increasing very rapidly.

The real challenge with regard to migratory waterbirds is to guarantee that protected sites are adequate and are adapted as needed over a large geographical area (Boere and Taylor 2004). In this sense, the rice fields located in the middle basin of the River Guadiana in Extremadura need to be protected by legal mechanisms to ensure their role as functional wetlands for migratory waterbirds. Recently, we proposed to the Regional Government the designation of the rice fields as a Special Protection Area for birds in Extremadura. The management of this important site (e.g., hunting regulation, and artificial flooding in dry winters using water from adjacent reservoirs) would guarantee the existence of a large area of functional wetlands which can play an important role in mitigating the loss of natural wetlands for populations of waterbirds using EAF.

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Impact of wind turbines on birds in Zeebrugge (Belgium)

Significant effect on breeding tern colony due to collisions

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Abstract We studied the impact of a wind farm (line of 25 small to medium sized turbines) on birds at the eastern port breakwater in Zeebrugge, Belgium, with special attention to the nearby breeding colony of Common Tern *Sterna hirundo*, Sandwich Tern *Sterna sandvicensis* and Little Tern *Sterna albifrons*. With the data of found collision fatalities under the wind turbines, and the correction factors for available search area, search efficiency and scavenging, we calculated that during the breeding seasons in 2004 and 2005, about 168 resp. 161 terns collided with the wind turbines located on the eastern port breakwater close to the breeding colony, mainly Common Terns and Sandwich Terns. The mean number of terns killed in 2004 and 2005 was 6.7 per turbine per year for the whole wind farm, and 11.2 resp. 10.8 per turbine per year for the line of 14 turbines on the sea-directed breakwater close to the breeding colony. The mean number of collision fatalities when including other species (mainly gulls) in 2004 and 2005 was 20.9 resp. 19.1 per turbine per year for the whole wind farm and 34.3 resp. 27.6 per turbine per year for 14 turbines on the sea-directed breakwater. The collision probability for Common Terns crossing the line of wind turbines amounted 0.110–0.118% for flights at rotor height and 0.007–0.030% for all flights. For Sandwich Tern this probability was 0.046–0.088% for flights at rotor height and 0.005–0.006% for all flights. The breeding terns were almost not disturbed by the wind turbines, but the relative large number of tern fatalities was determined as a significant negative impact on the breeding colony at the eastern port breakwater (additional mortality of 3.0–4.4% for Common Tern, 1.8–6.7% for Little Tern and 0.6–0.7% for Sandwich Tern). We recommend that there should be precautionary avoidance of constructing wind turbines close to any important breeding colony of terns or gulls, nor should artificial breeding sites be constructed near wind turbines, especially not within the frequent foraging flight paths.

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Keywords Birds · Collision · Disturbance · Gulls · Impact · Mortality · Terns · Wind turbine

Introduction

Wind turbines can have a negative impact on birds. Several European field studies have shown that birds can collide with the turbines during local and seasonal migration, or they can become disturbed in their breeding, resting and foraging areas or during migration (Langston and Pullan 2003; Kingsley and Whittam 2005).

In commission by the Flemish government, in May 2000 the Research Institute for Nature and Forest started monitoring the impact of wind turbines on birds. Preliminary study results (until 2001) were presented in Everaert et al. (2002) and Everaert (2003).

One monitoring location is situated in the outer port of Zeebrugge, Belgium ($51^{\circ}22' N$, $3^{\circ}13' W$), at the North Sea coast. There are 25 small to medium sized turbines in two lines placed alongside the water on the eastern port breakwater; 10 turbines of 200 kW (13–22 in Fig. 1), 12 turbines of 400 kW (1–12 in Fig. 1) and 3 turbines of 600 kW (23–25 in Fig. 1). In 2000, the construction of a peninsula was started next to 4 of the most northern 400 kW wind turbines. In the first phase, the peninsula was about 2 ha, in 2001 an additional 3 ha was constructed, in 2004 there was an extension to about 6.5 ha, and during the breeding season in 2005, the peninsula measured about 8.5 ha. The peninsula was created as an alternative breeding site for terns and plovers to compensate for the loss of other nearby areas

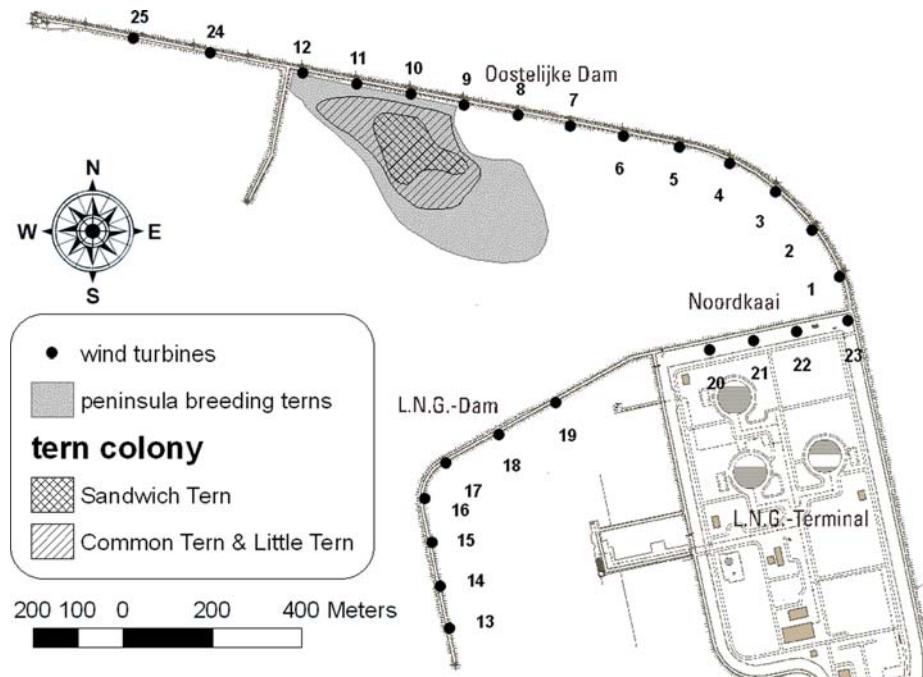


Fig. 1 Wind farm and tern colony on the eastern port breakwater in Zeebrugge. ‘Oostelijke Dam’ with 14 sea directed turbines. ‘Noordkaai’ and ‘LNG-Dam’ with 11 land directed turbines

at the western port breakwater (1500–3000 m west of the peninsula) where during the breeding season also a gull colony is present. The extension of the peninsula was assumed to be the only possible alternative in the short term (Courtens and Stienen 2004). As a result of the expansion of the peninsula at the eastern port breakwater and loss of habitat near the western port breakwater, in 2004 the numbers of terns at the peninsula strongly increased (Table 1).

Methods

Mortality

During 2004 and 2005, weekly or twice weekly searches for collision fatalities were performed under the wind turbines. Only the obvious or highly probable collision fatalities were used to determine the mortality (birds with lacerations, wing injuries, head injuries, back injuries and signs of internal injuries which were certainly or most probably caused by a collision). The range of the search circle was for all the turbines at the eastern port breakwater the same as the tip height of the 400 kW turbines (50 m), but not this whole area could be searched (see further). During the breeding season of the terns, more frequent searches were performed, sometimes daily (at least 3–4 times a week) and the search area was extended (Fig. 2). All useful information (date, collision victim, possible date of collision, species, age, sex, place/distance in relation to the nearest wind turbine, situation of the birds (wounds), etc.) was collected in a standardised database and spatially presented in a geographical information system (ArcMap in ArcGIS 9). In some cases, the distance between the nearest wind turbine and the location of the found collision victim was measured with a Leica Geovid 7 × 42 BDA, but often the distance was estimated by counting the number of steps to the nearest turbine.

Not all collision fatalities are found; some end up in the water next to the port breakwater and some are removed by predators. The estimated number of collision fatalities (Table 2) was therefore calculated using correction factors for available search area, search efficiency and scavenging (predation), deduced from Winkelmann (1992a).

The correction factor for available search area for each wind turbine was calculated in ArcGIS with the most recent aerial photograph of the area, and was applied

Table 1 Number of breeding pairs of terns on the peninsula along the eastern port breakwater ($=N_a$) and the total number in Zeebrugge including nearby areas in the western port and Heist ($=N$). '% N_1 ' is the percentage of the biogeographical population of the species that breeds in Zeebrugge, and '% N_2 ' is the percentage of the Belgian population that breeds in Zeebrugge (Stienen 2005; Wetlands International 2002)

| Year | Little Tern | | | | Common Tern | | | | Sandwich Tern | | | |
|------|-------------|-----|---------|---------|-------------|------|---------|---------|---------------|------|---------|---------|
| | N_a | N | % N_1 | % N_2 | N_a | N | % N_1 | % N_2 | N_a | N | % N_1 | % N_2 |
| 2001 | 126 | 184 | 1.62 | 100 | – | 2260 | 3.57 | 91 | – | 920 | 1.62 | 100 |
| 2002 | 70 | 145 | 1.28 | 100 | 12 | 2446 | 3.86 | 99 | – | 46 | 0.08 | 100 |
| 2003 | 150 | 152 | 1.34 | 88 | 257 | 2535 | 4.00 | 95 | – | 823 | 1.45 | 100 |
| 2004 | 138 | 172 | 1.52 | 98 | 1832 | 3052 | 4.82 | 90 | 4067 | 4067 | 7.18 | 100 |
| 2005 | 11 | 69 | 0.61 | 100 | 1475 | 1747 | 2.76 | 72 | 2538 | 2538 | 4.48 | 100 |

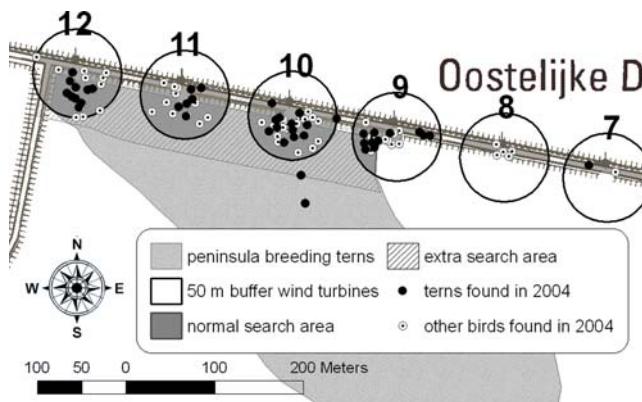


Fig. 2 Found collision fatalities on some of the 400 kW wind turbines (sea-directed breakwater near the peninsula) of the wind farm at the eastern port breakwater in Zeebrugge in 2004

Table 2 Used formula to determine the total number of collision fatalities (N_a = found number of collision fatalities, C_z = correction factor for search area ($=100/z$, where z = the proportion searched surface (in%) of the total surface which should have to be searched), C_p = correction factor for scavenging ($=100/p$, where p = the proportion of birds (in%) that were removed by predators during a scavenging-test, C_e = correction factor for search efficiency ($=100/e$, where e = the proportion of birds (in%) that were found by the investigator)

$$N\text{-estimated} = N_a^* C_z^* C_p^* C_e$$

for all collision fatalities (all species). The correction for scavenging was only used for small birds (wingspan smaller than a pigeon) and terns. In previous years, it was found that no correction factor for scavenging was necessary for larger birds. For small birds a correction factor of 7.14 was used (result of scavenging test in 2001, see Everaert et al. 2002). But because of the large number of collided terns since 2004, an extra test was performed to determine the predation on terns. In July 2004, 13 relatively fresh bird carcasses about the size of a Common Tern, 4 recently collided Common Terns and 2 Sandwich Terns were placed at the peninsula or on the road (port breakwater) next to it, and checked if the carcasses were still there after 2 days and further. The correction for search efficiency was only used for collided small birds and terns which were found on the peninsula. During March (small birds) and August (small birds and terns) in 2004, 28 bird carcasses were placed on the peninsula by one person. Within the next 24 h, another person who normally searches the area (author of this article) checked the peninsula as usual. It was concluded that no correction for search efficiency was needed for birds found at the road and on other clear areas. Hereafter, the ‘calculated number of collision fatalities’ will be called ‘number of collision fatalities’.

During two full days (including dawn and dusk) in June 2004 and 2005 (17 h each) with similar weather conditions (dry with wind W-ZW 2–4 Bft.), the number of terns flying from the colony towards the sea and back, thereby crossing the eastern port breakwater with the wind turbines, were determined in the zone of wind turbines 7–12, with a total baseline distance of 720 m (Fig. 2). The observer was located at the end of the baseline on the breakwater. The terns flying above the colony were not counted, only those who crossed the line of wind turbines or were flying very close

(< 30 m) to the wind turbines thereby quasi crossing the line. The data (mean number) of these diurnal movements were extrapolated for the whole month and combined with the calculated number of collision fatalities in June 2004 and 2005. With this, it was possible to determine the collision probability of the terns crossing the line of wind turbines on the eastern port breakwater. Additionally, in June 2004 and July 2005, 2 inspections were performed with a ‘generation 3’ night vision goggle ITT Night Enforcer 5000 (standard and additional 60–300 mm lens) to check if the terns were also performing nocturnal movements, but none were seen.

Disturbance

During the breeding seasons, the distance between the wind turbines and nesting terns was measured with a Leica Geovid 7 × 42 BDA. This data was also spatially presented in a geographical information system (ArcGIS). Additionally, during the whole year (mainly in winter), the distance between the wind turbines and foraging or resting birds (mainly ducks and other waterfowl) was measured.

Results

Mortality

The correction factor for available search area varied from 1.33 to 9.09 depending on the location of the wind turbine (visual example, see Fig. 2). The correction factor for scavenging was calculated to be 7.14 for small birds and 1.10 for all terns. The correction factor for search efficiency on the peninsula was 1.50 for small birds and 1.16 for all terns.

In 2004 and 2005, 121 resp. 105 collision fatalities were found, mainly gulls and terns. The total number of collision fatalities (corrected with the necessary correction factors) was calculated to be 523 resp. 459 birds, or 20.9 resp. 19.1 birds per turbine per year (Tables 3–4).

Tern mortality

Because of the large number of breeding terns on the peninsula since 2004, the daily number of terns crossing (or almost crossing) the eastern port breakwater was consequently high (Table 5).

Table 3 Number of collision fatalities from the wind farm at the eastern port breakwater in Zeebrugge in 2004, with the mean number per turbine per year. The ‘found’ numbers without correction factors are presented between brackets

| | Gulls + other large birds | Terns | Small birds | Total | Number per turbine per year |
|-------------------------------------|-------------------------------|---------------------|--------------------|----------------------|-----------------------------------|
| Sea directed turbines, $n = 14$ | 195.2 + 9.1 (54 + 1 found) | 156.8 (48 found) | 118.5 (4 found) | 479.6 (107 found) | 34.3 |
| Land directed turbines, $n = 11$ | 31.9 (12 found) | 11.5 (2 found) | 0.0 | 43.4 (14 found) | 3.9 |
| Total wind farm, $n = 25$ | 227.1 + 9.1 (66 + 1 found) | 168.3 (50 found) | 118.5 (4 found) | 523.0 (121 found) | 20.9 |

Table 4 Number of collision fatalities from the wind farm at the eastern port breakwater in Zeebrugge in 2005, with the mean number per turbine per year. The ‘found’ numbers without correction factors are presented between brackets

| | Gulls + other large birds | Terns | Small birds | Total | Number per turbine per year |
|------------------------------------|-------------------------------|---------------------|-------------------|----------------------|-----------------------------|
| Sea directed turbines, $n = 14$ | 138.7 + 1.7 (37 + 1 found) | 150.9 (51 found) | 95.3 (3 found) | 386.7 (92 found) | 27.6 |
| Land directed turbines, $n = 10^a$ | 62.5 (12 found) | 10.0 (1 found) | 0.0 | 72.5 (13 found) | 7.3 |
| Total wind farm, $n = 24$ | 201.3 + 1.7 (49 + 1 found) | 160.9 (52 found) | 95.3 (3 found) | 459.2 (105 found) | 19.1 |

^a One wind turbine was not operational during the whole year due to an accident where all blades were lost.

Table 5 Daily number of flights crossing or almost crossing the line of wind turbines in the zone of turbines 7–12 on the eastern port breakwater during the day in June 2004 and 2005. Mean number of 2 days of 17 h each

| Height range | Little Tern | | Common Tern | | Sandwich Tern | |
|--------------|-------------|-----------|-------------|------------|---------------|-------------|
| | June 2004 | June 2005 | June 2004 | June 2005 | June 2004 | June 2005 |
| 0–15 m | 1508 (86%) | 130 (35%) | 9548 (92%) | 3062 (72%) | 14090 (92%) | 10724 (87%) |
| 16–50 m | 216 (12%) | 240 (64%) | 650 (7%) | 1154 (27%) | 942 (6%) | 1596 (13%) |
| > 50 m | 25 (2%) | 5 (1%) | 65 (1%) | 12 (1%) | 205 (2%) | 14 (0%) |
| all heights | 1749 | 375 | 10263 | 4228 | 15237 | 12334 |

^a16–50 m = rotor height of the wind turbines

The increased number of foraging flights since 2004 resulted in a similar increase in the number of collision fatalities among the terns (Table 6). In the period from the beginning of May up to the middle of August 2004, in total 50 tern collision fatalities were found, the majority of it in May–July when the terns performed most movements between the breeding colony and the feeding grounds at sea. No collided

Table 6 Number of collision fatalities of terns at the wind turbines alongside the eastern port breakwater, Zeebrugge, during the breeding season. Corrected number = corrected for available search area, search efficiency, and scavenging

| Year | Found number of collision fatalities | | | | Corrected number of collision fatalities | | | |
|-------------------|--------------------------------------|-------------|---------------|-------|------------------------------------------|-------------|---------------|-------|
| | Little Tern | Common Tern | Sandwich Tern | Total | Little Tern | Common Tern | Sandwich Tern | Total |
| 2001 ^a | 2 | 3 | 0 | 5 | 8 | 20 | 0 | 28 |
| 2002 ^a | 2 | 4 | 0 | 6 | 9 | 15 | 0 | 24 |
| 2003 ^a | 3 | 6 | 0 | 9 | 10 | 32 | 0 | 42 |
| 2004 | 3 | 35 | 12 | 50 | 5 | 109 | 54 | 168 |
| 2005 | 1 | 41 | 10 | 52 | 2 | 129 | 30 | 161 |

^aIn 2001, 2002 and 2003, no correction for search efficiency and scavenging was used, but the correction for available search area was larger than the one used in 2004 and 2005 because of the fact that during the breeding season of 2001, 2002 and 2003, not all necessary search-areas on the peninsula (breeding area) were searched completely (see Everaert et al. 2002)

terns were found during the rest of the year. All found fatalities were adults. With the necessary correction factors for the available search area, scavenging (removal by predators or other animals), and search efficiency, the total number of collision fatalities is calculated to be 168 terns, or 1.57 per day. In the period from the middle of April up to the end of July 2005, similar results were found, with a total number of 161 terns, or 1.51 per day.

In 2004, 90% of the tern fatalities that were effectively found (76% of corrected number) came in collision with the 4 wind turbines which are located alongside the peninsula (turbines 9–12, see Figs. 1–3). In 2005, this was 92% (75% of corrected number, see Fig. 4). These turbines stand approximately perpendicular on the flight route of the terns crossing the eastern port breakwater. Both in 2004 and 2005, a significant difference (Kolmogorov–Smirnov Test, $P < 0.005$) in tern collision fatalities was found between the group of wind turbines alongside the peninsula (turbines 9–12) and the other group (turbines 1–8 and 13–25).

During the 4 (2 + 2) observation days in June 2004 and 2005 (to determine the number of movements crossing the line of wind turbines near the peninsula) we ‘witnessed’ 5 collisions ourselves (2 Common Terns and 3 Sandwich Terns). This means that at least 1.25 terns collided during one day. Additionally 3 Common Terns and 2 Sandwich Tern were seen colliding with one of the wind turbines during other shorter visits at the site in 2004 and 2005.

With the data of 48 fresh tern fatalities (died < 24 h before), found under the wind turbines alongside the peninsula (turbines 8–12) between May–August 2005, the mean diurnal wind direction (Dumon 2006) for the presumed collision-period was checked. It was calculated that 44 (91.67%) of these tern fatalities collided with NNW-ENE or SSE-WSW wind, and 4 (8.33%) with ENE-SSE or WSW-NNW wind. Between May–August 2005, there were 68.51% diurnal periods of 10 min with NNW-ENE or SSE-WSW wind and 31.49% diurnal periods with ENE-SSE or

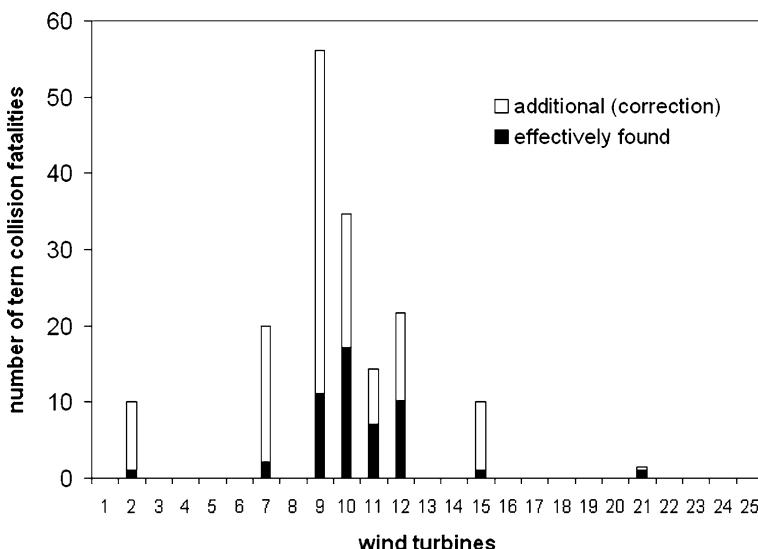


Fig. 3 Number of collision fatalities of terns per wind turbine on the eastern port breakwater, Zeebrugge, in 2004. The numbers of turbines correspond with those mentioned in Fig. 1

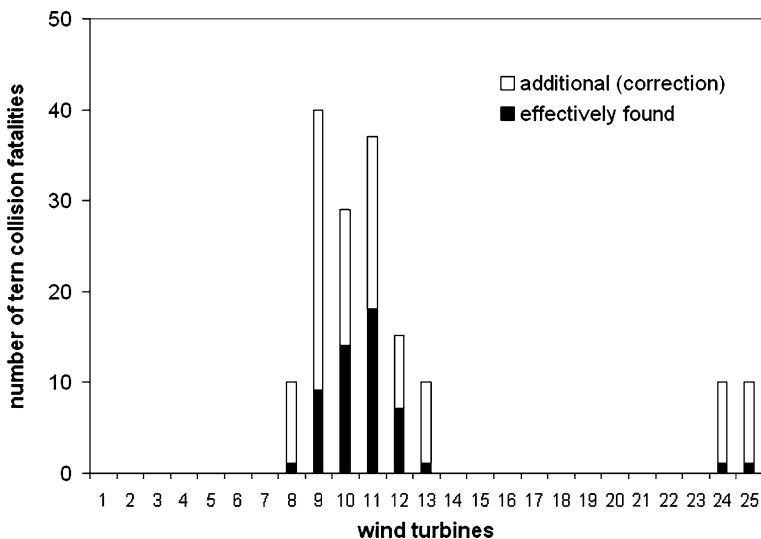


Fig. 4 Number of collision fatalities of terns per wind turbine on the eastern port breakwater, Zeebrugge, in 2005

WSW-NNW wind (Dumon 2006). The difference between the observed number of collision fatalities in the 2 subdivided wind directions (44 vs. 4) and the expected number (33 vs. 15) based on the total number (48) and the wind directions between May–August, was significant ($\text{Chi-Square} = 11.73$, $P < 0.001$). Concluding, the chance for a collision was higher during NNW-ENE or SSE-WSW wind with the turbine blades standing perpendicular on the flight route of the terns.

A significant correlation was found between the number of breeding pairs in the tern-colony and the number of collision fatalities ($P < 0.01$ for Common Tern, $P < 0.001$ for Sandwich Tern, see also Figs. 5, 6).

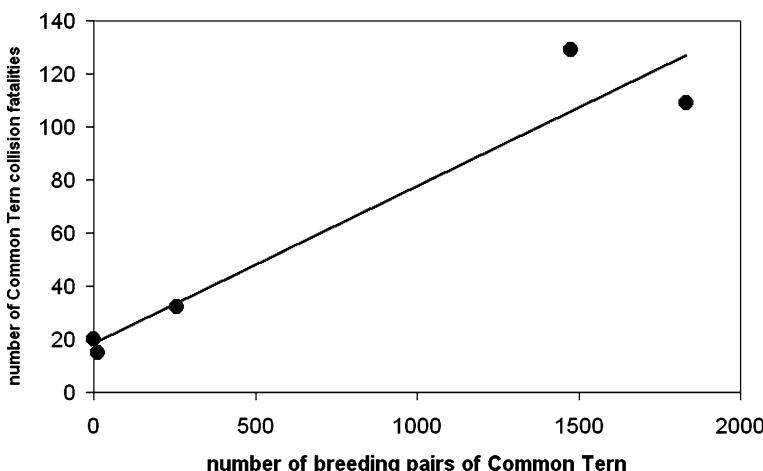


Fig. 5 Correlation between the number of Common Tern pairs in the breeding colony and the number of collision fatalities in the years 2001–2005 ($r = 0.96$; $P < 0.01$)

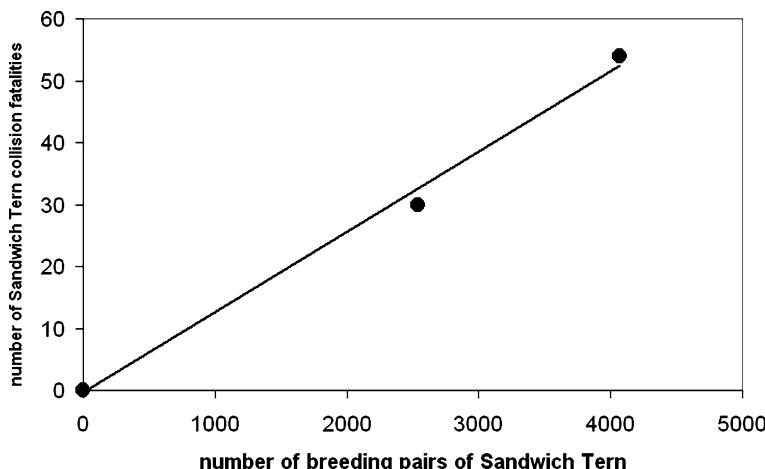


Fig. 6 Correlation between the number of Sandwich Tern pairs in the breeding colony and the number of collision fatalities in the years 2001–2005 (in 2001–2003 there were no breeding birds on the peninsula ($r = 0.998$; $P < 0.001$)

We observed that during the breeding season the line of wind turbines at the eastern port breakwater didn't act as a barrier for the foraging flights of the terns and gulls.

The collision probability for Common Terns crossing the line of wind turbines amounted 0.110–0.118% for flights at rotor height and 0.007–0.030% for all flights. A lower collision probability was found for Sandwich Tern, with 0.046–0.088% for flights at rotor height and 0.005–0.006% for all flights (Table 7).

In the breeding population at the eastern port breakwater, the wind turbines caused an additional mortality of 3.0–4.4% for Common Tern, 1.8–6.7% for Little Tern and 0.6–0.7% for Sandwich Tern (Table 8).

Disturbance of breeding, foraging or resting birds

In 2004, the nearest Common Terns were breeding at 30 m distance from the turbines, but the majority of the Common Terns, Little Terns and Sandwich Terns were breeding 100 m or further away from the turbines (Fig. 1). In 2005, most of the Sandwich Terns and many Common Terns were breeding at 50 m distance or further. Kentish Plover *Charadrius alexandrinus* and Common Ringed Plover

Table 7 Collision probability for Common Tern and Sandwich Tern in June 2004 and 2005. Calculated from the corrected number of collision fatalities on wind turbines 7–12 (near Tern peninsula) in June, and the number of diurnal flights across the eastern port breakwater in the zone of wind turbines 7–12 in June (extrapolated from the mean number of flights during 2 days in June, see also table 5)

| | Collision probability with diurnal flights at rotor height | | Collision probability with diurnal flights at all heights | |
|---------------|------------------------------------------------------------|--------|-----------------------------------------------------------|---------|
| | 2004 | 2005 | 2004 | 2005 |
| Common Tern | 1/848 | 1/911 | 1/13387 | 1/3338 |
| Sandwich Tern | 1/1130 | 1/2176 | 1/18283 | 1/16819 |

Table 8 Impact of the number of wind turbine fatalities (adult) on the breeding population of terns in 2004 and 2005 (eastern port breakwater and total of Zeebrugge)

| | Little Tern | | Common Tern | | Sandwich Tern | |
|-------------------------------------------------------------------------------------------------------|----------------|------------------------|----------------|----------------|----------------|----------------|
| | adults 2004 | adults 2005 | adults 2004 | adults 2005 | adults 2004 | adults 2005 |
| Eastern port breakwater (peninsula) | 276 | 22 + ca.8 ^a | 3664 | 2950 | 8134 | 5076 |
| Total Zeebrugge (incl. Western port & Heist) | 344 | 138 | 6104 | 3494 | 8134 | 5076 |
| Number of fatalities | 5 | 2 | 109 | 129 | 54 | 30 |
| Number of fatalities in % of the total breeding population on the eastern port breakwater | 1.8% | 6.7% | 3.0% | 4.4% | 0.7% | 0.6% |
| Number of fatalities in % of the total breeding population in Zeebrugge | 1.5% | 1.5% | 1.8% | 3.7% | 0.7% | 0.6% |

^aIncluding non-breeding birds, present during the breeding season

Charadrius hiaticula were breeding at about 40 m or further from the turbines, but were sometimes foraging at closer distances.

Large groups of non-breeding foraging/resting waterfowl and shorebirds normally held a distance of about 100–300 m from the turbines. Individual birds and small groups were sometimes closer (Table 9).

Discussion

Mortality

Research results of individual wind farms can not be generalised. In general, the collision mortality is related to the number of (flying) birds present, whereas the size of the turbines seems less important. Large modern turbines of 1500 kW or more can have as much or even more collision fatalities than smaller turbines (Akershoek et al. 2005; Everaert 2003; 2006). However, more data on large wind turbines is urgently needed.

The average number of collision fatalities in different European wind farms on land varies between a few birds per turbine per year up to 64 birds per turbine per year (Langston and Pullan 2003; Everaert 2006). Also within a wind farm the impact can strongly differ between individual turbines, indicating that ‘site selection’ can play an important role in limiting the number of collision fatalities. During previous years, for some wind turbines at the eastern port breakwater in Zeebrugge, up to 111 and 125 fatalities were calculated as a result of the correction factors for some small birds that were occasionally found (Everaert et al. 2002; Everaert 2003). In Sylt and Helgoland, Germany (each with only one wind turbine), after a full year study, bird deaths per turbine per year were estimated to be respectively 2.8–103 and 8.47–309 (Benner et al. 1993). One example of multiple bird kills occurred at a wind turbine in Nasudden, Sweden, where 49 collided birds were found after one night with poor

Table 9 Nearest observed distance to the wind turbines of non-breeding foraging or resting waterfowl and shorebirds at the peninsula and direct surroundings on the eastern port breakwater in Zeebrugge

| Species (-group) | Distance (m) of individual or small groups | Distance (m) of large groups (> 50 ex.) |
|--------------------------------------------------|--------------------------------------------|-----------------------------------------|
| Great Crested Grebe <i>Podiceps cristatus</i> | 50 | 100 |
| Cormorant <i>Phalacrocorax carbo</i> | 25 | ? |
| Grey Heron <i>Ardea cinerea</i> | 200 | ? |
| Little Egret <i>Egretta garzetta</i> | 100 | ? |
| Eurasian Spoonbill <i>Platalea leucorodia</i> | 200 | ? |
| Gulls <i>Larus spec.</i> | <10 | ? |
| Terns <i>Sterna spec.</i> | <10 | 50 |
| Common Shelduck <i>Tadorna tadorna</i> | 100 | ? |
| Mallard <i>Anas platyrhynchos</i> | 100 | 250 |
| Gadwall <i>Anas strepera</i> | 150 | 300 |
| Northern Shoveler <i>Anas clypeata</i> | 100 | 250 |
| Tufted Duck <i>Aythya fuligula</i> | 150 | ? |
| Greater Scaup <i>Aythya marila</i> | 150 | ? |
| Pochard <i>Aythya ferina</i> | 150 | ? |
| Northern Pintail <i>Anas acuta</i> | 100 | 250 |
| Eurasian Wigeon <i>Anas penelope</i> | 100 | 250 |
| Common Eider <i>Somateria mollissima</i> | 50 | ? |
| Red-breasted Merganser <i>Mergus serrator</i> | 100 | ? |
| Oystercatcher <i>Haematopus ostralegus</i> | 50 | 200 |
| Dunlin <i>Calidris alpina</i> | 150 | 250 |
| Common Ringed Plover <i>Charadrius hiaticula</i> | <10 | ? |
| Kentish Plover <i>Charadrius alexandrinus</i> | <10 | ? |
| Eurasian Curlew <i>Numenius arquata</i> | 100 | ? |
| Bar-tailed Godwit <i>Limosa lapponica</i> | 200 | ? |

? = not of application/not known

weather conditions; the turbine was not operational at the time, but was lit with a single lamp 10 m above the ground (Gill et al. 1996; Karlsson 1983). Overall, mortality events of this magnitude are seldom recorded, but with more and bigger wind turbines planned (certainly offshore), it is still unclear if this will only be a rare phenomenon. More intensive searches during the whole year and with many wind turbines at different types of locations are urgently needed.

Some researchers reported (almost) only common species (Winkelman 1992a; Van der Winden et al. 1999). However, the situation depends on the location. Even the presence of relatively low numbers of rare birds doesn't always guarantee a low collision probability. In Germany researchers already found 17 White-tailed Eagles *Haliaeetus albicilla* and 69 Red Kites *Milvus milvus* during occasional searches and the numbers are still increasing every year (Hötker et al. 2004; Dürr 2006). The find of 4 White-tailed Eagles between August and December 2005 in the new wind farm on the Island Smola, Norway (68 turbines) is also worrying and deserves attention (Follestad 2006). Wind turbine locations with relatively large numbers of protected birds of prey or song-birds, as in Tarifa and Navarra (Spain), Altamont Pass California are examples of poorly sited wind farms (SEO/Birdlife 1995; Lekuona 2001; Smallwood and Thelander 2004; Langston and Pullan 2003; Hötker et al. 2004). We must also take into account that the cumulative impact will increase with a growing number of wind turbines (Langston and Pullan 2003). More wind farms means an extra pressure superimposed to the already existing sources of disturbance.

Towards the situation for migrating birds, Kaatz (2002) recommended not to build large wind turbines on the coast, because of disturbance (barrier) but especially because of the possible large numbers of collision fatalities of which the biggest part of the small birds just get squashed totally during a collision with the rotors, whereby they can't be found on the ground. Even for large wind turbines the speed of the rotors goes to about 230 km/h at the tips. Therefore, the estimated collision of small birds using searches of dead birds on the ground (as with most studies) isn't totally reliable, even with corrections for scavenging and search efficiency. The only—known to us—comprehensive study whereby the collision chance for nocturnal migrating birds was calculated by means of the actual observed collisions (thermal image intensifiers) was performed in The Netherlands (Winkelman 1992b). The results there showed a remarkable high nocturnal collision probability of 1 on 40 (2.5%) passing birds at rotor height.

Daily searches for collision fatalities during the migration periods, together with systematic field observations of passing birds, could lead to a better picture of the behavior and collision chances of small birds. Observation methods by means of night vision devices and/or radar and thermal image intensifiers are a necessity. The recent developments of a full automatic sound- and image-detection system for collisions, with contact microphones on the turbine mast in combination with web cams (Verhoef 2003), and the thermal animal detection system (TADS) for estimating collision frequency of migrating birds at wind turbines (Desholm 2005) are also promising, but optimisation of these techniques is still necessary. Certainly given the current worldwide offshore wind energy plans, a reliable technique for general use is urgently needed.

Tern mortality

The European Birds Directive requires that Member States of the EU take appropriate measures for deterioration of the important bird areas, and to prevent disturbance in these areas, as far as these are of substantial (significant) influence. Terns are K-strategists, meaning that they are long-lived and raise a relatively small number of young annually (slow reproduction). For this reason these birds are sensitive for external factors causing an additional mortality for adults. Various authors have valued the annual mortality of adult Common Terns. Local mortality was 8 and 10%, and estimates based on mark-recapture analysis varied between 7 and 12% (Becker and Ludwigs 2004). For some long-lived species, more than 0.5% additive mortality could be a considerable impact (Dierschke et al. 2003). Population models revealed that significant decreases in size of bird and bat populations may be caused by relatively small (0.1%) additive increases in annual mortality rates, provided they are counteracted by density dependent increases in reproduction rates (Hötker et al. 2004). An environmental assessment for a proposed wind farm at the western port breakwater in Zeebrugge, concluded that the estimated additive mortality of 1% and higher in the local tern population of Zeebrugge, would be a significant impact on that population (see 10.3. & 10.4. in BMM 2004).

Given the biological importance of the breeding tern colony in Zeebrugge, it is prudent, and consistent with legal and regulatory policy, to consider the described biological impact of the wind farm at the eastern port breakwater in Zeebrugge to be significant, and to require substantial measures to avoid, minimize, or otherwise compensate to offset this impact. The best measures in the short term would be to

temporary shut down some of the turbines close to the breeding colony where most foraging flights occur, or to allocate the terns to a safer site in the future. It is contradicting that at other locations in Belgium and elsewhere, huge efforts are made to preserve some small colonies of Common Terns while at the same time a similar number of collision fatalities is allowed in the large colony in Zeebrugge.

In 2004 and 2005, the diurnal collision probability for Common Terns, flying at rotor height (Table 7) was similar to the result that was found in 2001 (1 on 600, see Everaert et al. 2002). The 2004/2005 difference in collision chance for Common Terns flying at all heights is contradicting, but it should be noted that in 2001 a collision chance of 1 on 3000 was found similar to the results in 2005. The contradicting figures found in 2004 may be caused by differences in wind and other weather conditions. The lower collision probability for Sandwich Terns may be due to the fact that Sandwich Terns mainly flew in a straight line towards the feeding grounds and back, whereas Common Terns had more irregular flight paths and performed more circling movements around the colony.

Relatively long lines of wind turbines or large wind farms can become an important barrier on the local and seasonal migration routes of non-breeding birds (diving duck's: Van der Winden et al. 1996; Wigeon *Mareca penelope*: Poot et al. 2001; Common Crane *Grus grus*: Brauneis 2000; seasonal migrating birds in general: Albouy et al. 2001; Richarz 2002; Langston and Pullan 2003). For certain birds the disturbance on their local migration routes could remain limited. Van den Bergh et al. (2002) concluded that a line of wind turbines at the Maasvlakte in The Netherlands didn't act as a barrier for the daily migration routes (foraging) of local breeding gulls and terns. Results from the turbines at the eastern port breakwater in Zeebrugge confirm this finding. Most terns in this study performed no or very small changes of course, before crossing the line of wind turbines (see also Everaert 2003).

Disturbance of breeding, foraging or resting birds

The fact that in 2004 some peripheral nests of terns (30 m and further) were closer to the wind turbines than the centre of the colony (>100 m), was most likely the consequence of the type of habitat (vegetation) and not because of a possible disturbance effect of the wind turbines. During the breeding season in 2005, many nests of the Sandwich Tern were located closer at 50–100 m distance. This suggests that the disturbance factor is relatively low for breeding terns, although effects on reproductive output have not been studied.

The observed distances with some other foraging or resting birds (especially shorebirds) can partially be also the consequence of specific habitat use (water line) on the peninsula. The results show that large groups of non-breeding waterfowl and shorebirds held a larger distance than individual or small groups of birds. Some studies on non-breeding birds have found significant disturbance for several duck species up to 300 and 400 m from wind turbines, and for some other waterfowl and shorebirds like geese up to at least 600 m (Langston and Pullan 2003; Kingsley and Whittam 2005).

General recommendations

Our study results clearly show that reasonable amounts of gulls and terns can collide with wind turbines, which seems to be a consequence of their quasi undisturbed

flight and breeding behavior. We recommend that there should be precautionary avoidance of constructing new wind turbines close to any important breeding colony of terns or gulls, nor should artificial breeding sites be constructed near wind turbines, especially not within the frequent foraging flight paths.

An exhaustive study before the selection of future wind farm locations is a key factor to avoid deleterious impacts of wind farms on birds. In general, current knowledge indicates that there should be precautionary avoidance of locating wind farms in all important bird areas and/or migration routes.

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The Iberian ibex is under an expansion trend but displaced to suboptimal habitats by the presence of extensive goat livestock in central Spain

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Abstract In this paper an updated distribution of the Iberian ibex (*Capra pyrenaica*, Schinz 1838) in the central Spanish region of Castile-La Mancha is shown. The species is present in 19% of the study region, and in areas not cited so far in the literature. A detailed analysis of habitat suitability was also carried out, applying a new methodology, Ecological-Niche Factor Analysis, which uses presence data to build a habitat suitability map of a given species. As livestock activity is quite intense in the region, the presence of a potential competitor, the domestic goat (*Capra hircus*), was included in the analyses. Factors affecting ibex relative abundance were determined by means of a nested stepwise multiple regression, where livestock presence/absence was the nested factor. The presence of livestock has a negative effect on ibex relative abundance, causing the ibex to select areas of poor, sparse vegetation, cultivated lands and forests, whereas in the absence of livestock, the ibex is mainly present in pasture-scrub lands and non-cultivated lands. Conservation implications of these results are discussed in the context of a Mediterranean region where extensive livestock grazing systems abound.

Keywords Biodiversity conservation · *Capra hircus* · *Capra pyrenaica* · Livestock grazing system · Habitat displacement · Habitat suitability analysis · Resource competition

Introduction

To conservation biologists it is of particular interest to determine the effects of invasive species on the natural history of autochthonous ones (see Lodge 1993). A particular example is that of exotic ungulates introduced in areas where they can potentially compete with native ones (see, e.g., Cassinello et al. 2004). Among the

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former, livestock represent a particular instance (Voeten and Prins 1999), usually underestimated by conservation biologists (Fleischner 1994). Although livestock graze more than one-third of the world's land area, and in many instances share resources with native ungulates (see de Haan et al. 1997), evidences of a negative impact on the latter are not conclusive and highly debated (e.g., Saberwal 1996; Mishra and Rawat 1998; Madhusudan 2004; Young et al. 2005).

The development of large, relatively permanent, agriculture-based societies was the primary event initiating livestock domestication about 10,000 years ago (Price 2002). With a few exceptions, ungulate domestication (e.g., cattle, sheep and goats) mainly began in the Near East (Troy et al. 2001). The presence of livestock in Europe goes back to Neolithic times, domestic sheep and goats showing up particularly in Mediterranean countries (see, e.g., Martín Bellido et al. 2001).

The status and distribution of the Iberian ibex have been studied by several authors, either in the whole peninsula (e.g., Granados et al. 2002; Pérez et al. 2002) or in some particular areas (e.g., Granados et al. 1998; Palomares and Ruiz-Martínez 1993; Lasso De La Vega 1994; Pérez et al. 1994; Gortazar et al. 2000). Concerning Castile-La Mancha region, in central Spain, Granados et al. (2002) indicate that the ibex is distributed exclusively in 11% of the region, whereas Pérez et al. (2002) distinguish 51 ibex population nuclei in Spain, out of which only 4 were located in Castile-La Mancha: Serranía de Cuenca, Cabañeros National Park, Sierra de Alcaraz (connected to the well established ibex population of Sierra de Cazorla, Segura y Las Villas Natural Park, it is supposedly in expansion), and Sierra Madrona (a series of fragmented nuclei connected to other ones in Sierra Morena, Jaén province).

Here, we analyse the current distribution and habitat use of the Iberian ibex (*Capra pyrenaica*, Schinz 1838) in Castile-La Mancha. We have considered it appropriate to use a political division to define our study area because in Spain conservation field is partly ruled by regional governments. This region is characterised by an intense livestock breeding activity, namely extensive sheep and goat grazing systems (see Martín Bellido et al. 2001). We have, thus, included in our analyses the presence of the domestic goat (*Capra hircus*), a close relative of the Iberian ibex and, therefore, expected to share feeding habits and ecological requirements with it; to our knowledge, no comparative studies of diet and/or spatial niche use have been made so far. Sheep, on the contrary, show a differing feeding behaviour (Martínez 2002) and probably their potential as competitor of the Iberian ibex is less pronounced.

The spatial prediction of species distribution is an important tool for conservation biology and management planning (e.g., Hortal et al. 2005; Whittaker et al. 2005). Developments of ecological and biogeographic theories have been translated into different methodologies, which are able to predict the distribution ranges and habitat suitability of species (see Guisan and Zimmermann 2000; Ferrier et al. 2002; Scott et al. 2002), using a wide variety of statistical approaches and Geographical Information Systems tools (GIS) (e.g., Austin 2002; Rushton et al. 2004). The use of a Digital Elevation Model (DEM) constitutes a basis for generating maps of environmental variables (see Guisan and Zimmermann 2000), as it has basic outcomes, such as altitude, slope or aspect, which influence the distribution of the organisms. Furthermore, the use of digitalised land information database, allows a more detailed analysis of factors determining species distribution.

Predictive models can easily be made from data of the presence and absence of a given species (e.g., Osborne and Tigar 1992; Brito et al. 1999). Nevertheless, it is necessary to distinguish true absences from a mere lack of information (Thuiller et al. 2004; Araújo et al. 2005). The determination of true absences of a given species in a given area is the main problem of many animal presence/absence data sets (Hirzel et al. 2002; Zaniewski et al. 2002). Thus, some techniques incorporate presence-only data (Hortal et al. 2005), such as the relatively novel Ecological Niche Factor Analysis (ENFA) (Hirzel et al. 2002). ENFA is used to determine habitat suitability starting from the location of presence-only data. These maps are the result of the location of a given species within the multidimensional environmental area that is defined by considering all mapping units within the study area (Guisan and Zimmermann 2000). These habitat suitability maps indirectly reveal the species potential distribution (Hirzel et al. 2002). This approach is recommended when absence data are not available (most data banks), unreliable (most cryptic or rare species) or meaningless (invaders) (Hirzel et al. 2001), the subsequent results are to be handled with caution (e.g., Brotons et al. 2004; Engler et al. 2004). Using these data, this method characterises the realised niche of the species from a set of environmental predictors. Thus, an application of the method could be interesting in many domains: landscape management for endangered species, better knowledge of unknown or inaccessible areas, or also better knowledge of ‘new species’ ecology and/or distribution (e.g., Reutter et al. 2003; Gallego et al. 2004; Chefaoui et al. 2005). This method was originally assessed in the Alpine ibex (*Capra ibex*) (Hirzel et al. 2002), but is currently widely used (see a list of publications at <http://www.unil.ch/biomapper/bibliography.html>).

Apart from an updated distribution of the Iberian ibex in Castile–La Mancha, our aim in this study is to carry out a detailed analysis of habitat suitability of the species and determine which factors affect its abundance taking into account the influence of livestock presence/absence.

Materials and methods

The study area

Located in central Spain, it corresponds with Castile–La Mancha political division (U.T.M. 30S 294,348–681,063 4,208,706–4,575,340), which is placed at the southern plateau of the Iberian Peninsula. Politically, the region is conformed of five provinces (see Fig. 1), where the study species is distributed unevenly. Castile–La Mancha is the Iberian region where game activity is more intense. It has a surface area of 79,226 km², which represents 15.7% of the whole Spanish territory. The area devoted to game activity in this region is 70,000 km² (88% of its territory), big game estates occupying 19,000 km² (Junta de Comunidades de Castilla–La Mancha, <http://www.jccm.es/medioambiente/mednat/cazapesca.htm>).

The study region shows a typical Mediterranean continental climate, with dry periods both in summer and winter, rains concentrated in autumn and spring, and extreme temperatures during the hottest (summer) and coldest (winter) seasons. Mediterranean woodland vegetation is present and it is formed of oak trees (*Quercus ilex*) along with shrubs of different species (e.g., *Q. coccifera*, *Pistacia lentiscus*, *Cistus* spp., *Rosmarinus officinalis*, etc.). Open lands with

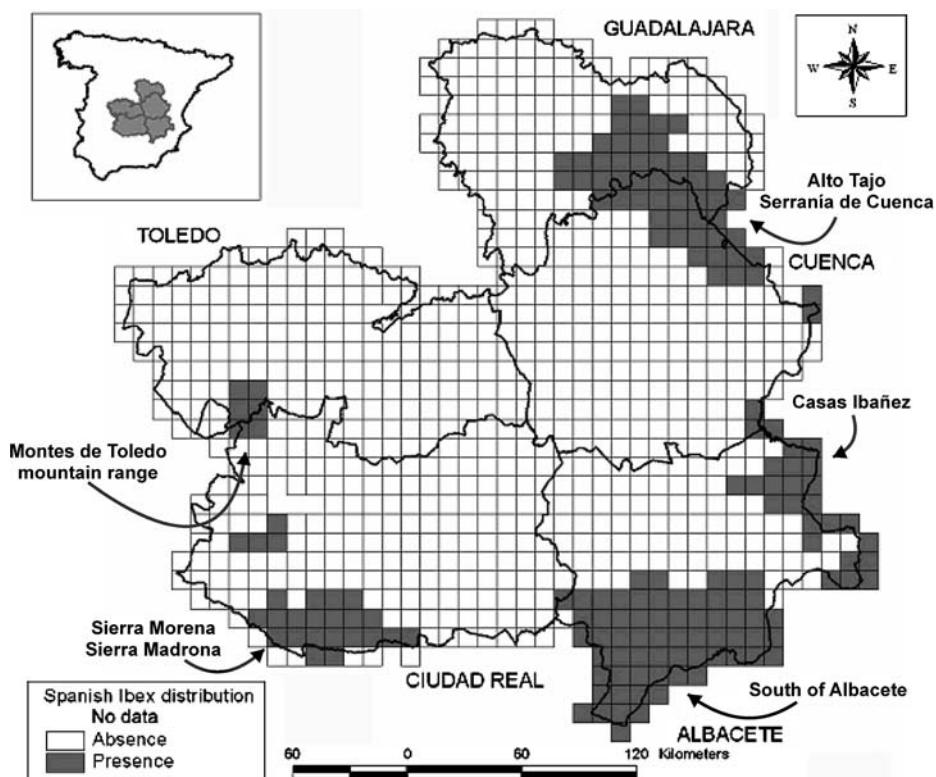


Fig. 1 Situation of the study area (Castile-La Mancha region in central Spain), the administrative provinces concerned, and its division in 10×10 grids, showing the presence/absence of the Iberian ibex

scattered trees (evergreen oak savannah like habitats), the so-called “dehesas”, are also common. In addition, pine woodlands (*Pinus* spp.) can also be found in some elevated areas.

Apart from the Iberian ibex, other ungulate species that can be found free-ranging in the study area are wild boar (*Sus scrofa*) and red deer (*Cervus elaphus*), and to a lesser extent fallow deer (*Dama dama*), and roe deer (*Capreolus capreolus*) (see, respectively, Rosell and Herrero 2002; Carranza 2002; Braza 2002; San José 2002).

The study species

The Iberian ibex is a wild goat endemic to the Iberian Peninsula. The IUCN (2004) considered it as at Low Risk, but near threatened (LR/nt), whereas the existing subspecies hold different qualifications. *C. p. victoriae* Cabrera, 1911 is Vulnerable (VU D2), due to the few and small areas it inhabits (see Pérez et al. 2002). *C. p. hispanica* Shimpfer, 1848 is at Low Risk (LC/cd), but its viability depends on current conservation programmes. This latter subspecies is widely distributed compared to the former one (*ibid*). Two other subspecies were also distinguished, but they are extinct nowadays: *C. p. pyrenaica*, Schinz 1838 and *C. p. lusitanica*, Schlegel

1872 (*ibid*). However, the distinction of these subspecies has been questioned by Manceau et al. (1999), who found no genetic differences between the two existing subspecies.

The sampling method

Presence of ibexes in the study area was assessed by means of direct field observations and by carrying out surveys ($n = 149$) addressed to forest rangers and staff from environmental agencies of the government of Castile-La Mancha region. Information obtained by other naturalists was verified by visiting areas where ibexes were reported. The sampling units were 10×10 km. UTM grid cells ($n = 905$).

Survey addressees were asked to draw in a map their work area and the range occupied by the Iberian ibex, red deer, wild boar and livestock. A questionnaire was given to them, where they indicated the status of the populations present, such as the largest group size registered, a straightforward variable, easy to account for by field watchers.

In order to assess ibex abundance, we firstly relied on forest rangers and environmental managers' indication of the largest group size registered. The Iberian ibex is characterised by sexual segregation through most of the year, but the largest group sizes are attained during the mating season (November–December) according to Granados (2001), when ibexes are also more conspicuous. We have confirmed that group sizes given in the questionnaire refer to mixed groups observed during the mating season, when they may reflect population abundance in species showing sexual segregation (see Toigo et al. 1996). In addition, we validated these data by carrying out our own field surveys.

During September 2003, we performed 17 field surveys consisting of line transects (e.g., Burnham et al. 1980), a methodology widely used to estimate relative abundance of wild goats (e.g., Alados and Escós 1996; Pérez et al. 1994). Average length of line transects was 3 km., and they were carried out in the main areas where the Iberian ibex is present in Castile-La Mancha, and during hours of maximum activity, i.e. at dawn and at dusk (e.g., Alados 1986). We only registered female groups, and used these data to test whether the largest group size obtained in the questionnaire was a good estimate of ibex abundance (see Results).

Habitat suitability

The ENFA computes a habitat suitability model by comparing the ecogeographical variables (EGVs) which characterise the locations where the species is detected with those present in the whole study area (Hirzel et al. 2002).

Habitat suitability for the Iberian ibex was assessed in the area where the species was more abundant according to the surveys, using 1×1 km UTM grid cells. Twenty-seven EGVs were defined, including topographical features (e.g., altitude, slope), land cover, and livestock presence (see Table 1), and normalised by a Box-Cox transformation (Sokal and Rohlf 1981). We did not consider climatic variables because of the relative homogeneity of the study area on this matter, where only slight differences can be registered, mainly due to topographic variations. Average distances to each land cover classes were calculated for each sample unit by means of “Distance Operator” tool (Idrisi32 v.32.21) (see Hirzel et al. 2002). The topographic data from a DEM carried out by the Shuttle Radar Topography Mission

Table 1 Ecogeographical variables (EGVs) used in the ENFA

| Codes | Meaning | Global mean | Species mean |
|---------------------|--------------------------------------------|-------------|--------------|
| Topographic | | | |
| altitud_max | Maximum altitude | 507.24 | 0.95 |
| Aspect | Average orientation | 98.49 | 0.87 |
| Slope | Average slope | 2.82 | 1.44 |
| Cultures | | | |
| dist_agriculture | Average distance to cultivated lands | 2260.56 | 0.82 |
| dist_agroforest | Average distance to agroforest lands | 11990.41 | 1.22 |
| dist_annual_crops | Average distance to annual crops | 19572.28 | 0.63 |
| dist_complex_cult | Average distance to complex cultures | 1933.19 | 0.64 |
| dist_perm_irrigate | Average distance to irrigated cultures | 1368.97 | 0.42 |
| Fruit tree | | | |
| dist_fruit_tree | Average distance to fruit tree cultures | 4249.16 | 0.15 |
| dist_olives | Average distance to olive tree cultures | 5388.66 | 0.04 |
| dist_vineyards | Average distance to vineyards | 4714.15 | 1.25 |
| Woodland | | | |
| dist_broad_leav | Average distance to broad leaves forests | 4828.36 | 1.05 |
| dist_mixed_forest | Average distance to mixed forests | 6194.78 | 0.72 |
| dist_conniferous | Average distance to conniferous forests | 3021.63 | -0.34 |
| dist_wood_scrub | Average distance to wood-scrub ecotones | 1509.38 | 0.81 |
| dist_sclerophyllous | Average distance to sclerophyllous areas | 1421.79 | 0.34 |
| Scrubland | | | |
| dist_moors_heath | Average distance to moors and heaths areas | 29133.07 | 0.56 |
| Grassland | | | |
| dist_natu_grass | Average distance to natural grass lands | 2706.51 | 0.39 |
| Sparse veg. | | | |
| dist_sparse_veg | Average distance to sparse vegetation | 12196.57 | -0.32 |
| dist_bare_rocks | Average distance to bare rocks areas | 24583.19 | -0.05 |
| Infrastructure | | | |
| dist_village | Average distance to villages | 3217.65 | 0.84 |
| dist_industr | Average distance to industrial areas | 11612.99 | 1.07 |
| dist_road_rail | Average distance to roads and rails | 27601.89 | 0.74 |
| Water | | | |
| dist_river | Average distance to rivers | 10852.34 | -0.09 |
| dist_inland_marshes | Average distance to inland marshes | 20417.79 | 1.38 |
| dist_water_bodies | Average distance to water bodies | 14409.52 | 0.09 |
| Livestock | | | |
| dist_goat_livestock | Average distance to goat livestock | 2515.05 | 0.07 |

Average values in the study region are shown (global mean), together with the standardized ones, as provided by ENFA, in areas where the Iberian ibex is present (species mean). All values are in metres, except for orientation, which is in degrees

(European Environment Agency 2000), with a spatial resolution of 90 m., was extracted by overlaying the DEM with the cells of 1 × 1 km. in a geographic information system (Idrisi32 v32.21) (see Hortal et al. 2001).

Firstly, the ENFA was run, by means of BioMapper software (Hirzel et al. 2001, 2004; see <http://www.unil.ch/biomapper/>). It computes a global marginality coefficient, expressing how, on all the EGVs, the species average differs from the global average, and a global specialisation coefficient, expressing the ratio of global variance to species variance.

Formally, marginality is defined as the absolute difference between the global mean and the species mean, divided by the standard deviations of the global distribution multiplied by a constant (see Hirzel 2001 for details). A value close to one

means that the species lives in a very particular habitat relative to the reference set. Similarly, specialisation is defined as the ratio of the standard deviation of the global distribution to that of the study species (Hirzel 2001). A randomly-chosen set of cells is expected to have a specialisation of one, while any value exceeding that score indicates some form of specialisation.

The factor coefficients for the marginality factor account for the marginality of a given species in each EGV considered. It is measured as units of standard deviations of the global distribution. The higher the absolute value of a coefficient, the further the species departs from the average value of a given EGV. There are other factors which express a degree of specialisation, where the higher the value, the more restricted is the range of the study species on the corresponding variable (Hirzel 2001).

Habitat use

Information obtained from the surveys was registered in 10×10 km. UTM grid squares ($n = 905$) by means of Idrisi32 v32.21 software (Clark Labs, Clark University). For each UTM square the frequency of occurrence of 11 ecogeographical variables (EGVs) were identified (see Table 2). These variables were obtained from CORINE Land Use/Land Cover database, spatial resolution (pixel width) of 250 m (European Environment Agency 1996). From this information we carried out both the habitat use analysis and the study of the influence of goat livestock.

The analysis of the variables which determine habitat use (Table 2) by the Iberian ibex was assessed by a nested stepwise multiple regression analysis, using domestic goats presence/absence as the nested factor (e.g., Quinn and Keough 2002). The Iberian ibex abundance was the response variable. We designed a three step procedure to clarify the significance of the variables and their interaction with goat livestock on the Iberian ibex habitat use.

In total, 11 habitat factors were considered: (1) We discarded a number of variables with no statistical significance and avoided multicollinearity by using the

Table 2 EGVs used in habitat use analysis for the Iberian ibex relative abundance dependent variable

| Variables | Meaning | Significance |
|-------------------|----------------------------------------------|--------------|
| Goat livestock | Presence/Absence of goat livestock | ** |
| Highest altitude | Maximum altitude (m) | n.s. |
| Average altitude | Average altitude (m) | n.s. |
| Slope | Average slope index | n.s. |
| Cultures | Frequency of cultures per pixel | * |
| Woodland | Frequency of woodlands per pixel | ** |
| Scrubland | Frequency of scrublands per pixel | ** |
| Grassland | Frequency of grasslands per pixel | n.s. |
| Sparse vegetation | Frequency of sparse vegetations per pixel | ** |
| Infrastructures | Frequency of human infrastructures per pixel | n.s. |
| Water reservoir | Frequency of rivers per pixel | * |

The significance level of step 2 is provided (** $P < 0.01$, * $P < 0.05$, n.s. = non-significant). See text and Table 1 for more details

Spearman Rank Correlation coefficients. (2) Each of the independent variables obtained from step 1 were then related to the dependent variable, ibex relative abundance. Stepwise multiple regression analysis was used (Quinn and Keough 2002). (3) Variables that yielded $P < 0.05$ in step 2 were integrated into a final model which also included the nested factor of livestock presence. We carried out a nested regression analysis and obtained a final model through a backward stepwise procedure. The level of significance for step 3 was set at 5%. The statistics package used was SPSS 10.06.

Results

Species distribution according to the surveys

Information covering 97.68% of the whole Castile-La Mancha region has been obtained from 149 surveys correctly filled in. Results showed that the Iberian ibex is present in 19% of the study area (175 out of 905 sampling units). Five population nuclei have been identified: Montes de Toledo mountain range, Sierra Madrona—Sierra Morena, Alto Tajo—Serranía de Cuenca, Casas Ibáñez, and south of Albacete (see Fig. 1). The species is more widely distributed in Albacete province (it is present in 47% of the territory), followed by Guadalajara (21%), Cuenca (15%), Ciudad Real (12%) and Toledo province (3%).

Habitat suitability

An habitat suitability map for the study species was carried out for the province of Albacete, where the species was more abundant (see above). This meant a total number of 15,384 1 × 1 km. UTM grid cells. Table 1 shows average values for the EGVs that define the habitat, both in the whole study area (global mean) and in the area where ibexes were found (species mean, with standardised values). For the ENFA analysis, the variable “average distance to non-irrigated lands” was discarded due to its discontinuity. The three significant factors selected (out of 27) explained 87.6% global marginality and 75.2% global specialisation. Coefficients of relationship between variables and each one of the three factors are shown in Table 3.

Global marginality was 2.03, and global tolerance was 0.49. The habitat suitability map can be seen in Fig. 2. The first factor obtained, marginality factor, was essentially associated to both high altitudes and slopes, and areas distant to agro-forest lands, broadleaf woodlands, industrial areas, marshes and vineyards (see coefficients in Table 3). Ibexes are extremely sensitive to shifts from their optimal conditions on this axis. Next factors show a certain degree of specialisation, being associated to areas distant to coniferous forests, sparse vegetation and human constructions, such as roads and railways, but also close to annual crops lands. Factor 3 accounts for 19.2% of specialisation, so that information provided is much less accurate than that of the other two factors (see Table 3).

Habitat use

Relative ibex abundance was assessed by the largest size group registered in each UTM grid cell considered in the study area, and obtained from the questionnaire.

Table 3 Correlation between ENFA factors and the environmental descriptors (EGVs)

| Variable | Factor 1 (87.6%) | Factor 2 (55.4%) | Factor 3 (19.2%) |
|---------------------|---------------------|---------------------|---------------------|
| altitud_max | 0.24 | 0.01 | 0.10 |
| Aspect | 0.22 | 0.04 | 0.00 |
| dist_agriculture | 0.21 | 0.08 | -0.02 |
| dist_agro_forest | 0.31 | -0.09 | 0.32 |
| dist_annual_crops | 0.16 | -0.26 | 0.16 |
| dist_broad_leav | 0.26 | -0.02 | 0.00 |
| dist_goat_livestock | 0.02 | -0.06 | 0.20 |
| dist_coniferous | -0.09 | 0.51 | 0.61 |
| dist_industr | 0.27 | 0.09 | 0.23 |
| dist_inland_marshes | 0.35 | -0.02 | -0.37 |
| dist_road_rail | 0.19 | 0.42 | 0.11 |
| dist_sparse_veg | -0.08 | 0.62 | -0.27 |
| dist_villages | 0.21 | -0.09 | 0.04 |
| dist_vineyards | 0.31 | 0.12 | -0.14 |
| dist_water_bodies | 0.02 | 0.03 | -0.34 |
| dist_wood_scrub | 0.20 | -0.01 | -0.01 |
| slope | 0.36 | 0.04 | 0.01 |

Percentages indicate the amount of specialization accounted for by each factor.
Factor 1 is Marginality factor

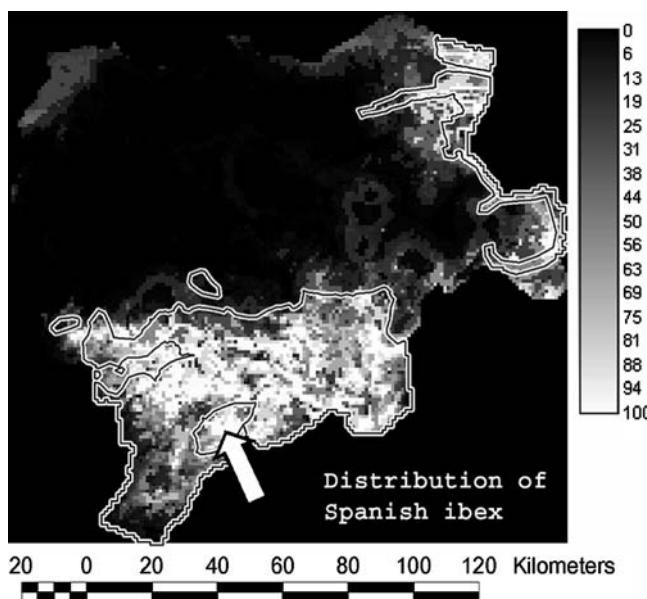


Fig. 2 Habitat suitability map for the Iberian ibex in Albacete province. Observed Ibex distribution is outlined. The arrow indicates a potentially suitable area not occupied by the ibex, and where livestock is present

Previously, we determined the validity of this measure by relating it to our own average group size (see above). In our field surveys, we detected 36 ibex groups (167 animals were counted) from the 17 transects carried out in September 2003. The average group size was 4.76 ± 0.65 , and it correlated with the largest group size obtained in the questionnaire (Spearman Rank Correlation: $n = 9$, $\rho = 0.80$, $P = 0.01$), so that the latter can be considered as an estimate of ibex abundance.

Table 4 Final model obtained for the habitat use analysis for the Iberian ibex relative abundance dependent variable (nested stepwise regression output)

GL column refers to goat livestock absence (A) and presence (P). TE refers to the typical error

| Parameter | GL | Estimate | TE | t | Probability |
|-------------------|------|----------|------|-------|-------------|
| Intercept | 3.07 | 0.86 | 3.58 | <0.01 | |
| Scrub land | (A) | 0.88 | 0.31 | 2.88 | <0.01 |
| | (P) | -0.94 | 0.30 | -3.13 | <0.01 |
| Cultures | (A) | -0.53 | 0.27 | -2.47 | 0.01 |
| | (P) | 0.89 | 0.19 | 4.67 | <0.01 |
| Wood land | (A) | -0.04 | 0.22 | -0.20 | 0.84 |
| | (P) | 0.81 | 0.22 | 3.65 | <0.01 |
| Sparse vegetation | (A) | -0.27 | 3.10 | -0.09 | 0.93 |
| | (P) | 1.45 | 0.45 | 3.19 | <0.01 |
| Water | (A) | 5.62 | 4.02 | 1.40 | 0.16 |
| | (P) | 12.55 | 6.14 | 2.04 | 0.04 |
| Goat livestock | (A) | -4.54 | 1.23 | -3.69 | <0.01 |
| | (P) | 0 | 0.00 | – | – |

Nested stepwise multiple regression analysis showed that livestock influences habitat use of the Iberian ibex, relegating it to suboptimal vegetation areas (see Table 4). In those grid cells where domestic goat livestock ranges in sympatry with the ibex, the latter occupies preferentially cultivated lands, sparse vegetation areas and forests; whereas in absence of livestock the ibex is mainly found in pasture–scrub areas and non-cultivated lands. The marginal effect caused by distance to goat livestock herds (see Factor 3 in Table 3), is exemplified in Fig. 2.

In Fig. 3 the relationship between those variables which showed opposite directions, depending on the presence/absence of goat livestock, i.e. scrub land and cultures, is shown.

Discussion

Here we have updated the Iberian ibex distribution in the region of Castile–La Mancha (central Spain). A habitat suitability model has also been accomplished by using the ENFA technique, particularly suitable for presence-only data of a given species. Our results indicate that the Iberian ibex is not occupying its optimal habitat in those areas where it shares its range with domestic goat herds.

On ibex distribution in the study region, it is noteworthy to point out a wider presence in comparison with previous surveys (Alados 1997; Pérez et al. 2002). A plausible explanation is the expected increase of the species area of distribution which is taking place nowadays, in part due to a natural increment of population numbers due to habitat changes, game management translocations (Gortazar et al. 2000) or its recovery from past sarcoptic mange epizootics (Pérez et al. 1997), and a probable decrease of its hunting pressure caused precisely by the incidence of this disease (see Garrido 2004).

Concerning risks associated to parasite infections of the ibex, the main agents are host-inspecific, e.g., sarcoptic mange (Pérez et al. 1997), so that they can infect any ungulate species, among other mammals. Therefore, at high host densities, as it is the case in areas with high livestock densities, the availability of habitat for these parasites increases, as does the risk of epizootics (see Acevedo et al. 2005).

Specific values for marginality and tolerance indexes are bound to depend on the global set chosen as reference, so that a species might appear extremely marginal or

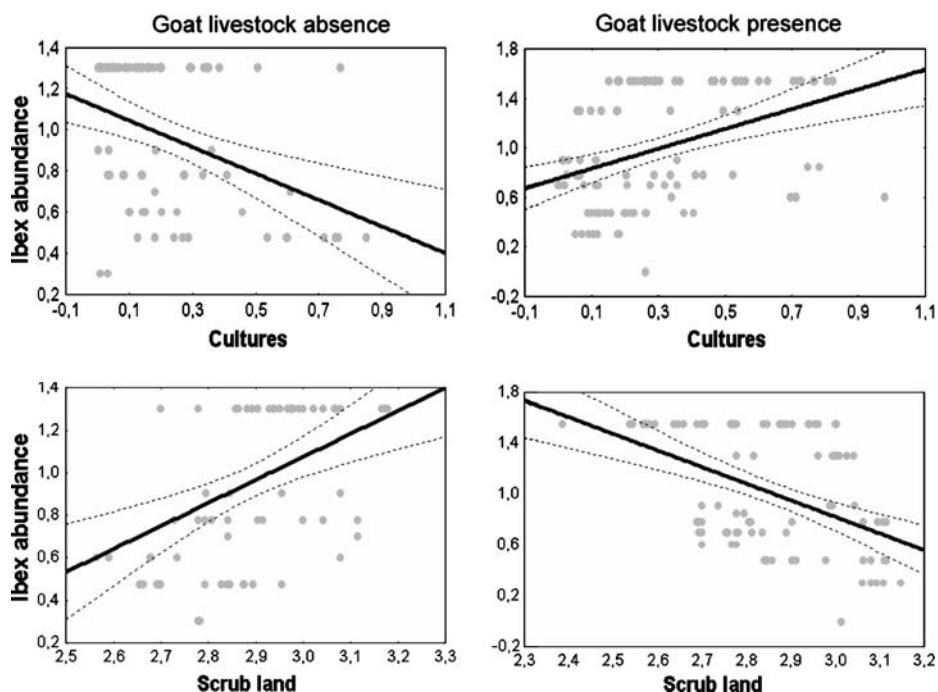


Fig. 3 Relationships between Iberian ibex relative abundance and two EGVs which show opposite directions depending on the presence/absence of goat livestock, i.e. scrub land and cultures (see Table 4)

specialised on the scale of a whole country, but much less so a subset of it (Hirzel et al. 2002). According to habitat suitability analysis carried out the Iberian Ibex is highly marginal in the studied area, and presents a medium tolerance, evidencing that, although it is placed in marginal areas in Castile-La Mancha, it seems to tolerate habitat changes, therefore compensating its marginality with the expansion to areas of relatively suboptimal habitat.

In our study, livestock seem to compete and displace the Iberian ibex from its optimal habitat, i.e. pasture-scrub lands (e.g., Chirosa et al. 2002), in those grid cells where livestock is present (see Fig. 2). We have no data on social avoidance between both species, so that future research should be focused on confirming this apparent ecological displacement. Similar conclusions were obtained from a study carried out in the Great Basin, where pronghorn (*Antilocapra americana*) avoided areas grazed by sheep during winter until spring-regrowth occurred, and favoured areas temporarily rested from sheep use (Clary and Holmgren 1982; Clary and Beale 1983).

This apparent displacement of the Iberian ibex to suboptimal habitats by livestock presence is confirmed in our nested factor analysis of habitat use. The results obtained indicate that the ibex occupies different habitats depending on the presence of domestic goats. When they are present, as seen in the previous analysis of habitat suitability, the ibex is preferentially found in suboptimal habitats, according to its resource requirements (see, e.g., Chirosa et al. 2002),

i.e. sparse vegetation, cultures and woodlands; whereas when livestock is absent, the ibex mainly uses scrub lands and non-cultivated areas, where food availability according to its diet is higher (e.g., Martínez and Martínez 1987; Martínez 2000).

The question is whether both species, the ibex and the domestic goat, actually compete for resources. Resource partitioning is defined as the differential use by organisms of resources such as food and space (Schoener 1974; Begon et al. 1996), and may explain how species coexist despite extensive overlap in ecological requirements (Hutchinson 1959; MacArthur and Wilson 1967; MacArthur 1972; May 1973). On the contrary, competition is considered to be the major selective force causing this differential use of resources (Schoener 1974, 1986).

As livestock range and distribution exceed any natural expansion process, they can be considered as introduced exotic species (see, e.g., Voeten and Prins 1999), and resource partitioning with native ungulates would not be expected but, rather, a certain overlap in resource selection (see Fleischner 1994; Edwards et al. 1996; Aagesen 2000; Prins 2000). This is the case in North American steppes, where livestock replaced the bison *Bison bison* and pronghorn (Schwartz and Ellis 1981; Hartnett et al. 1997). Thus, dietary niche divergence in sympatric species can occur even at a very subtle scale (Hartnett et al. 1997). Campos-Arceiz et al. (2004) found that food overlap between Mongolian gazelles (*Procapra gutturosa*) and livestock occurred not only at the main forage categories but also at the selection of plant parts for foraging.

Interpretation of measures of niche overlap in terms of the implications for competitive interactions is problematic (Putman 1996). High observed overlap can imply competition, but only if resources are limited. In fact, observations of high overlap might equally well be indicative of a lack of competition (see Schoener 1983; de Boer and Prins 1990; Putman 1996).

The implications these results may have on the Iberian ibex viability and expansion can be evaluated from different views. Ibex populations in the study region seem to be in expansion, particularly in the provinces of Albacete, Cuenca and Guadalajara, if we compare current abundance of the species (Fig. 1) and that of former studies (e.g., Pérez et al. 2002). Therefore, currently isolated populations might enter into contact. This may imply new viability risks associated to the increase of certain diseases, such as sarcoptic mange. This disease has already been detected sporadically in Albacete province (C. Gortázar Unpublished data), so that a consequent generalisation of its prevalence might occur in the near future. Finally, hunting pressure on the Iberian ibex is negligible in Castile-La Mancha: a 0.0004% (63 individuals) of total big game hunted in 1999–2003 period (Garrido 2004). Therefore, we believe that game activity is not currently disturbing the Iberian ibex expansion movements in the region.

As a conclusion, we encourage comparative studies of habitat use with other ungulate species in sympatry (including exotics), as well as a monitoring of disease prevalence and colonisation process in order to assure the establishment of the species in central Spain.

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Testing indicators of epiphytic lichen diversity: a case study in N Italy

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Abstract The predictability of a standardized and widely used biomonitoring method for estimating total lichen diversity on trunks (LDV-index) was tested. The study was carried out in Veneto (NE Italy), on 34 randomly selected trees in five sites in different landscape contexts. Two sets of biodiversity data were obtained from each tree: (1) the LDV index based on species frequency within a standard sampling grid positioned on a limited part of the trunks only (2) the total number of species found on the trunks. Total species richness on trunks is significantly related with the LDV index, which suggests that the LDV standard methodology can be used also for estimates of lichen diversity. Even a LDV index based on macrolichens, or on large-lobed foliose lichens only, still permits reliable estimates of total diversity on the trunks.

Keywords Biodiversity · Lichen Diversity Value · Macrolichens · Simple linear regression · Species richness

Introduction

Indicators of biodiversity are surrogates for total biodiversity estimates that can be more easily sampled (Noss 1990; Lawton et al. 1998; Lindenmayer et al. 2000; Will-Wolf et al. 2002; Bergamini et al. 2005). For example, Kerr et al. (2000) demonstrated that *Hymenoptera* morphospecies are valuable predictors of total species richness at the landscape scale in an oak savanna ecosystem. The selection of indicators, however, may be problematic (e.g. Landers et al. 1988; Noss 1990), and their relation with the overall diversity must be tested.

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There is already a standardized and widely used methodology for assessing lichen diversity used in the context of monitoring of air quality: the European guideline, recently proposed by Asta et al. (2002), based on the Italian protocol (AA.VV. 2001), and subsequently adopted with small modifications in Germany (VDI 2006). Lichen diversity is described by a biodiversity index (LDV = Lichen Diversity Value) based on species frequency within a standard sampling grid positioned on a limited part of the trunks only (Asta et al. 2002; Scheidegger et al. 2002). This index, which takes into account both species richness and abundance, proved to be highly related with atmospheric pollution (Amman et al. 1987), environmental quality (e.g. Castello and Skert 2005), and human health (Cislaghi and Nimis 1997). This methodology, which includes standardization of all phases of data collecting, might be successfully used in other contexts to estimate total lichen richness. However, experimental tests on the LDV are absent, and its reliability as a biodiversity indicator remains unknown.

Thus, the aims of the present study are (1) to test the predictability of the standard assessment of lichen diversity provided by the LDV method to the total species richness on the trunks of different tree species in different landscape contexts; (2) to test the reliability of the LDV index calculated on selected guilds of easily identifiable lichens for rapid surveys over large areas.

Materials and methods

The study was carried out in the Region of Veneto in northeastern Italy, which covers an area of 18,364 km² (Fig. 1). The landscape is formed of four principal units: Dolomites and Pre-Alps in the northern part, hills and plain in the southern part. More details on climate, vegetation, and human activities are in Nimis et al. (1991).

The sampling strategy follows the guidelines officially recognized by the Italian Agency for the Protection of the Environment (AA.VV. 2001), based on the standard protocol proposed by Asta et al. (2002). The grid density of sampling stations at national level is 18 km × 18 km. Each station (Principal Sampling Unit—PSU) is a square area of 1 × 1 km². In Veneto, 54 PSUs can be identified, and classified in five

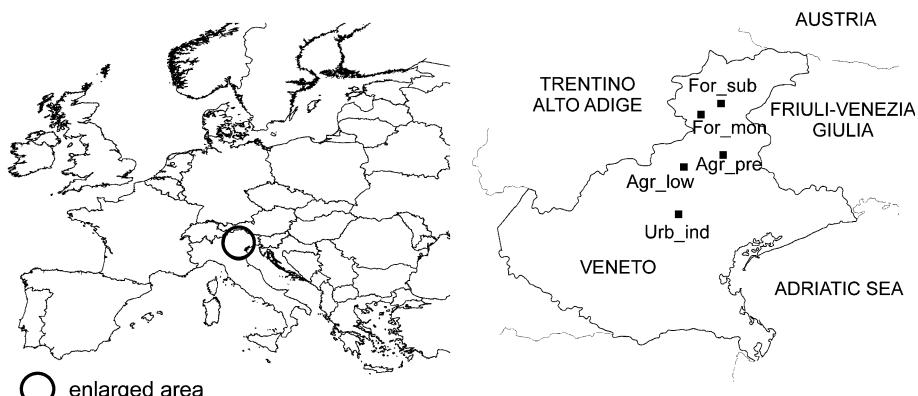


Fig. 1 Study area and location of the five PSUs

main environment types: (1) Urb_ind: urban, highly disturbed and industrialized areas; (2) Agr_low: low altitude agricultural areas; (3) Agr_pre: hilly and pre-alpine agricultural areas; (4) For_mon: montane forests; (5) For_sub: subalpine forests.

One PSU was randomly selected for each environment type. In each PSU, the trees were selected according to the procedures of the national protocol (AA.VV. 2001) within four circular subplots of 1 ha surface distributed in the four quadrants of the PSU. A total of 34 trees were sampled, with a minimum of 3 in For_mon, and a maximum of 10 in Agr_pre. In Table 1, the main characteristics of the five-selected PSUs are reported. The LDV method warns about comparing results across climatic and geographical gradients. However, this recommendation concerns the use of the LDV index as an estimator of air quality and not—like in our case—of total diversity. In the former case, it is important to minimize all factors other than air quality, which might influence lichen diversity; in the latter, it is important to test the predictability of the LDV index as an indicator of total diversity across a wide spectrum of ecological variation.

Within each PSU, a single tree species was used (Table 1). According to the national procedure (AA.VV. 2001), the sampling trees had to satisfy the following requirements: (1) minimum circumference 70 cm, (2) inclination of the trunks not exceeding 10°, (3) absence of evident factors of disturbance on the bark.

Two sets of biodiversity data were obtained from each tree: (1) partial biodiversity following the LDV method (AA.VV. 2001; VDI 2006), and (2) total biodiversity of the trunk. Following the LDV method, partial lichen diversity was sampled using the four standard frequency ladders of 10 cm × 50 cm divided into five 10 cm × 10 cm subplots, attached to the tree trunk at the cardinal points with the shortest side at 100 cm from the ground. All lichen species inside the ladders were listed and their frequency was computed as the number of subplots in which the species occur. The sum of the frequencies of all species found in the four sampling ladders of a single tree is the estimate of Lichen Diversity (LDV) of that tree. Total lichen diversity of the trunks was sampled by carefully exploring the whole surface of the trunks from the base up to 2 m, producing a complete list of species.

Simple linear regression was applied to check the power of the partial biodiversity estimates to predict the total species richness at trunk level. The relation among several LDV calculated on different species subsets with the LDV calculated with the methodology described in Asta et al. (2002) was also tested. Statistical analyses were carried out according to SAS Institute Inc. (1989).

Table 1 Characteristics of the five selected Principal Sampling Units (PSUs)

| Environment type ¹ | Urb_ind | Agr_low | Agr_pre | For_mon | For_sub |
|-------------------------------|--------------|----------------|----------------|--------------|--------------|
| Elevation (m a.s.l.) | 15 | 330 | 700 | 980 | 2.050 |
| Tree species | <i>Tilia</i> | <i>Juglans</i> | <i>Juglans</i> | <i>Larix</i> | <i>Larix</i> |
| No. of sampled trees | 7 | 5 | 10 | 3 | 9 |

¹Abbreviations refer to the environment types as in the text

Results

The first test compares LDV values with total species richness of the trunks (Fig. 2a). Since these parameters are strongly related ($R^2 = 0.74$), the LDV can be considered a predictive estimate of total species richness. The second test (Fig. 2b) shows that the bare number of species found within the sampling ladder is a good indicator of the total number of species on the trunks.

The predictability of selected guilds of species with respect to total species richness and to the LDV, was also tested. A significant relation was found between the number of macrolichens inside the sampling ladders and total species richness on the trunks (Fig. 3a), albeit with a lower explanatory capacity ($R^2 = 0.64$). Considering only large-lobed foliose lichens (e.g. *Parmelia* s.l.), the regression remains significant with a negligible loss of goodness of fit ($R^2 = 0.63$). Microlichens (crustose lichens) show a weaker relation ($R^2 = 0.57$) with the total species richness (Fig. 3b). Other guilds of species (e.g. fruticose lichens, narrow-lobed foliose lichens), and coverage values are not significantly related with total species richness. The best predictor of total species richness is the total number of species found within the sampling ladders. However, total species richness can be consistently predicted by the number of macrolichens and of large-lobed foliose lichens found within the sampling ladders. The LDV computed on macrolichens only is significantly related with that computed on all lichen species with an R^2 of 0.60 (Fig. 3c). The same regression computed with the LDV of microlichens had a R^2 of 0.39 (Fig. 3d). No significant relation was found with the LDV computed by large lobed foliose species.

Discussion

The LDV and the number of species found within the sampling ladders proved to be robust estimators to the total species richness on trunks in different landscape

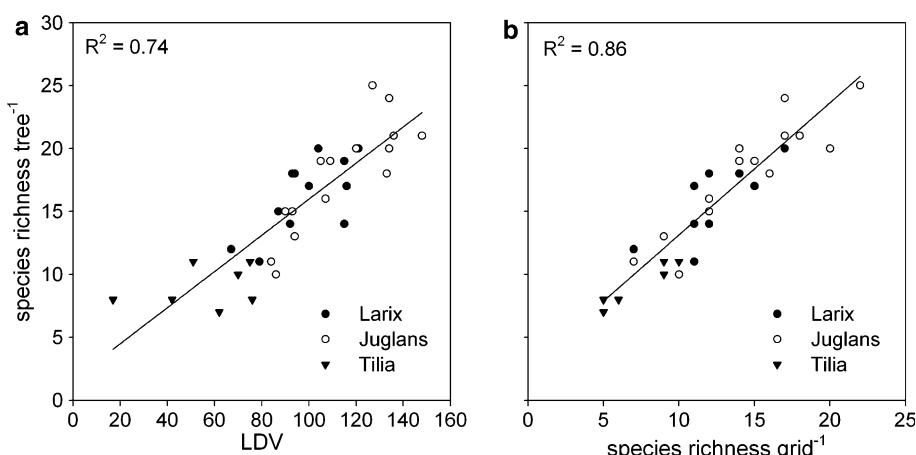


Fig. 2 Simple linear regression of total species richness on the trunk versus (a) LDV values, and (b) species richness within the sampling ladders. All analyses are significant at $P < 0.01$ (F -test). The symbols indicate the different tree species

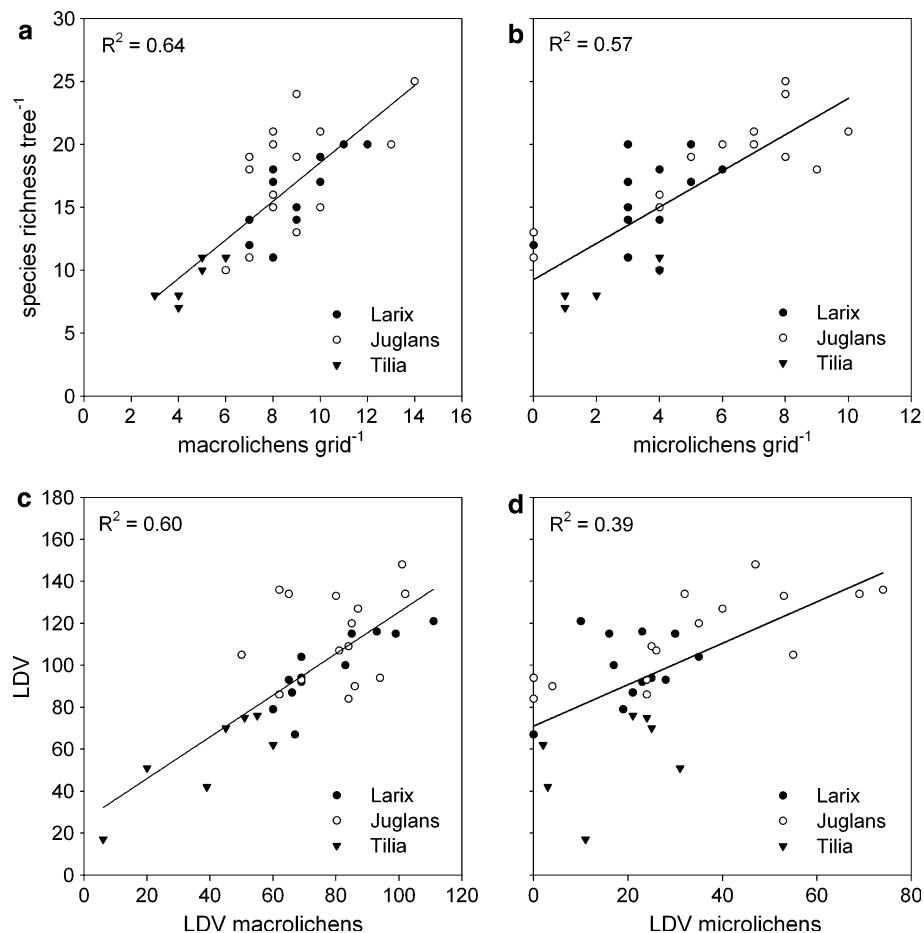


Fig. 3 Simple linear regression of total species richness versus (a) number of macrolichen species, and (b) number of microlichen species inside the sampling ladders; and linear regression of total LDV versus (c) LDV computed on macrolichens only, and (d) LDV computed on microlichens only. All analyses are significant at $P < 0.01$ (F -test). The symbols indicate the different tree species

contexts and on different trees. Species richness within grid and LDV values presented the lowest values on *Tilia* in the urban areas, while the largest values were found on *Juglans* in less disturbed agriculture areas. Despite such differences, reasonably related to the hosting trees and environment, the ratio of not sampled species is rather constant, indicating that this is not related to the overall flora at tree level. This suggests that the LDV standard methodology can be used not only for monitoring air quality, but also as a protocol to estimate total lichen diversity.

However, lichens are rather laborious to identify, since several crustose species need microscopic analysis and thin-layer chromatography for detecting secondary chemical compounds (Culberson and Culberson 1994). The risk of missing a species is higher for crustose lichens than for macrolichens: a non-specialist can miss about two third of the crustose species (Will-Wolf et al. 2002), which can result in a consistent source of bias (Brunialti et al. 2002).

When a robust regression model among the full dataset and more easily identifiable subsets of species can be demonstrated, it might be preferable to use a partial, but correct information whose uncertainty degree can be explicitly included in the results. The sampling and identification of macrolichens are actually much easier for non-specialists (McCune et al. 1997). Our results show that a partial sampling based on macrolichens, or even on large-lobed foliose lichens only, still permits reliable diversity estimates. The linearity of the relation indicates that the ratio of macrolichens on the total species richness is constant and independent from bark conditions and landscape contexts.

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Analysis and evaluation of ecosystem resilience: an economic perspective with an application to the Venice lagoon

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Abstract This paper focuses on the analysis and evaluation of resilience anchored in an economic perspective. Resilience, as well as most of the benefits provided by ecosystems, is not priced on current markets. However, this does not mean that resilience is of no value for humans. On the contrary, the interest of using an economic perspective, and the respective scientific methodology, will be put forward in terms of resilience relevance for ecosystem functioning, and its impact on human welfare. The economic perspective is anchored in an anthropocentric analysis evaluating resilience in terms of provision of natural capital benefits. These in turn are interpreted as insurance against the risk of ecosystem malfunctioning and the consequent interruption of the provision of goods and services to humans. For this analysis, we make use of a conceptual framework that identifies and describes the different value components of resilience. Finally, we present an illustration that discusses the economic analysis of resilience benefits in the context of the Venice Lagoon.

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Keywords Economic perspective · Economic value · Ecosystems' resilience · Ecosystems' thresholds · Natural insurance capital

Introduction

Ecosystems are described in the ecological literature as ‘biological communities that interact with the physical and chemical environment, with adjacent ecosystems and with the atmosphere’ (Holling et al. 1995, p. 54). From an economic perspective, ecosystem functioning and stability are responsible for the provision of a wide range of benefits to humans. Such benefits include provisioning, regulating and cultural services directly affecting people and supporting services needed to maintain other services (Millenium Ecosystem Assessment 2005).

In recent years, anthropogenic pressures are increasingly threatening ecosystem functioning and stability, and thus environmental quality. Increasing rates in the urbanisation trend and extractive land use management regimes, such as intensive monoculture agricultural practices, have contributed to unprecedented impacts on ecosystems. These, in turn, create additional uncertainty with respect to the inter-temporal provision of goods and services and in adapting to environmental change. As a result, we have been contributing to a growing interest in the identification and definition of policy-oriented strategies, ranging from prevention to adaptation measures, so as to deal with such pressures.

In order to guarantee the success of such policies, today more than ever both natural and social scientists are focusing their attention on the study of ecosystem functioning. On one hand, natural scientists analyse the conditions for ecosystem persistence, stressing the relevance of resilience in terms of the capacity of a natural system to maintain its functioning. In other words, resilience is here interpreted as a means to adapt to environmental changes or disturbances. On the other hand, economists are exploring a set of tools so as to identify and assess the value of resilience, measured in terms of its impacts on human welfare. In this context, resilience is interpreted as a natural insurance capital against the risk of ecosystem malfunctioning, and the consequent damages associated to a potential interruption of the ecosystems' ability to provide goods and services. This paper focuses on the analyses and evaluation of resilience anchored in an economic perspective.

The paper is organized as follows. Section ‘A natural science perspective on resilience’ introduces the concept of resilience as originally put forward in the ecological literature. Section ‘Motivations for economic valuation’ presents and discusses the motivations to perform economic valuation, in general, and non-market valuation of ecosystem resilience, in particular. Section ‘Resilience as a source of economic value’ defines and explains the concept of economic perspective, which will serve as the platform for the discussion and evaluation of resilience. Section ‘The Venice Lagoon case study’ presents an illustration. Section ‘Conclusion’ concludes.

A natural science perspective on resilience

Introduction

The concept of resilience has been applied in many different fields. In physics, for instance, it identifies the resistance of building materials to collision, by providing an

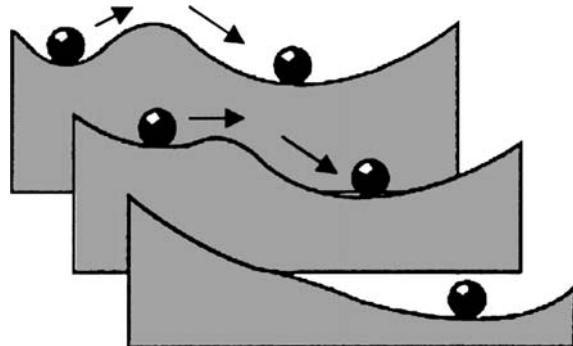
indicator of materials' fragility: a material poorly resilient is more fragile and *vice versa*. In the ecological literature, resilience, first defined by the theoretical ecologist Holling (1973), refers to the understanding of an ecosystem's dynamics, in general, and its conditions for persistence, in particular (Gunderson 2000). Abandoning the traditional equilibrium-centred ecological view, which focused on the static analysis of ecosystem equilibrium, Holling proposed a dynamic approach to the analysis of ecosystem functioning. From Holling's perspective, resilience is then defined as the amount of disturbance that can be absorbed before the system redefines its structure and respective processes, thereby moving the system from the current state to another state. This perspective is referred to in the literature as *ecological resilience* (Holling 1986, 1996).

Since the pioneering work of Holling, other versions of the concept of resilience have been put forward by natural scientists. Among them, is the definition proposed by Pimm (1984), who defines resilience as the time necessary for a system to return to an equilibrium once the system has been the target of an environmental change or disturbance. The respective amount of time gives an indication of the ecosystem's ability to assimilate the change, which is in turn inferred as a measurement of resilience. The faster is the recovery, the less is the time needed to return to equilibrium and therefore the stronger the resilience of the system. This perspective is referred to in the literature as *engineering resilience* (Holling 1986, 1996).

We can discuss in more detail each approach by exploring the use of Fig. 1, as originally proposed by Scheffer et al. (1993) and Carpenter et al. (1999).

The ball represented in Fig. 1 depicts the system state, the convex set represents the stability domain and the arrows represent the disturbances that the system is subject to. An equilibrium exists whenever the ball stops rolling after having experienced other positions induced by disturbances. In this setting, *ecological resilience* can then be defined as the maximum size of the ripples before the ball reaches the new equilibrium after perturbations occurred. On the other hand, *engineering resilience* can be thought as the return time of the ball to the initial equilibrium, i.e. to the bottom of the convex set, depending on the slope of the sides of the convex set. In both cases, resilience depends on the shape of the convex set, which is, as shown by the three slices represented in Fig. 1, subject to changes. These changes result from the alteration, often human induced, of parameters such as birth rates, death rates, carrying capacity, migration or per capita predation, governing interactions between the elements of ecosystems (Beisner et al. 2003).

Fig. 1 Ecological and engineering resilience. Source: Scheffer (1993), Carpenter et al. (1999)



As recently pointed out by Gunderson (2000), both perspectives, i.e. *ecological resilience* and *engineering resilience*, have in common the fact that both deal with aspects of stability of system equilibrium. In other words, both investigate the persistence of a system, which is supposed to operate near or close to an equilibrium state, concentrating on the self-organized behaviour of that natural system over time. On the other hand, the definitions offer alternative measures of the capacity of a system to maintain its functioning and stability.

Such differences reflect alternative assumptions about the existence of either single or multiple ecosystem equilibria. The *ecological resilience* perspective, which focuses on conditions far from any steady state, where instabilities can flip a system into another stability domain, implicitly assumes the existence of multiple locally stable equilibria and the tolerance of the system to perturbations that facilitate transitions among stable states. The lower the natural system's capacity to adapt to changes, the higher is the risk for the system to shift into a qualitatively different state. When such new state is undesirable, restoring the system to its previous state can be complex, expensive and sometimes impossible. In case of uncertainty and potential irreversibility of the change, the interplay between stabilizing and destabilizing forces is then particularly relevant for the maintenance of ecosystem functioning. When destabilizing forces are predominant, the natural system could be unable in the new qualitative state to guarantee to humans the provision of the same goods and services as in the previous state. From the ecological resilience perspective, particular attention is then focused on maintaining the existence of an ecosystem functions relevant to human welfare. The *engineering resilience* perspective instead assumes the existence of a global stability, meaning that the behaviour of a system remains within the stable domain containing a single steady state. From this perspective resilience does not affect which equilibrium the ecosystem will reach, but rather on how it will reach its equilibrium. As a consequence, the main emphasis is put on the efficiency of the path to reach the single best equilibrium steady state. The more resilient the ecosystem, the faster is the process of returning to the original equilibrium state, i.e. the higher is the probability of maintaining the efficiency in ecosystems' functioning. This indirectly implies that the variability of natural systems can be to a certain extent effectively controlled by humans and its consequences are, at least up to a certain point, predictable.

In order to analyse and value resilience, the next sub-section will be devoted to the identification and definition of resilience in relationship to species diversity and natural system functioning. In doing so, we will refer to the notion of ecological resilience: ecosystems' complexity and their unknowable and unpredictable evolution over time (Deutsch et al. 2002), which seems to be more realistically consistent with the existence of multiple local equilibria.

Resilience, system functioning and species diversity

Species diversity refers to the variety of species on earth, or in any smaller geographical area. Such diversity is associated with a large degree of uncertainty. In fact, estimates of the total number of species on earth range from 5 to 300 million, of which about 1.7 million have been described, and less than 0.5 have been analyzed in detail for potential economic benefit properties (Miller et al. 1985; CBD 2001). The best-catalogued species groups include vertebrates and flowering plants, with other groups, such as lichens, bacteria, fungi and roundworms, relatively under-researched

(Wilson 1988a; Pimm et al. 1995). A long-standing theoretical paradigm has hypothesized that species diversity is important because it enhances the productivity and stability of ecosystems (Odum 1950). In this stream of thought, some authors distinguish species according to their impact on ecosystem stability and resilience. In particular, Walker (1992) distinguishes two types of species, *drivers* and *passengers*. *Drivers* correspond to the species that directly or indirectly influence the ability of the ecosystem to function, to provide goods and services as well as to buffer against changes or disturbances in the future. *Passengers* correspond to the species that do not have a significant role in altering the states of the ecosystem. In this context, while removing *passengers* usually induces little effect in the system performance and absorption capacity, removing *drivers* may cause a large impact, threatening system resilience by reducing its buffering ability to absorb disturbances. The plant *Banksia prionotes* well illustrates Walker's notion of driver (Walker, 1995). In the wheatbelt in Western Australia, during a certain period of the year this plant is the only source of nectar. The loss of such a species would probably induce the loss of all the honeyeaters of the region and all the plants for which honeyeaters are vectors for pollen. The overall impact of *Banksia prionotes* loss on plant-species diversity in that area would then be substantial. In other areas where other species are flowering the effect would not be so critical. In the coastal regions of Western Australia, for instance, honeyeaters can find alternative sources of nectar in other *Banksia* species flowering at the same time. As a consequence, there the *Banksia prionotes* is not a driver species: its functional role is easily substitutable by other species.

Some recent studies, however, acknowledge that no pattern or deterministic relationship needs to exist between species diversity and the stability of ecosystems (Johnson et al. 1996). Others instead suggest that the stability of ecosystems, and thus resilience, may be linked to the prevalence of a rather limited number of organisms and groups of organisms that seem to drive or control the critical processes necessary for ecosystem functioning—known as *keystone species* (Paine 1969; Folke et al. 1996). The extinction of these species reduces the ecosystem's capacity to accommodate external shocks, like climatic and human influences, and ultimately results in the loss of spatial variety in ecosystem types. Therefore, analyzing keystone species is about determining the minimum range of species within which the different state variables can be disturbed without flipping from the current ecosystem to another regime of behaviour (Perrings and Opschoor 1994; Holling et al. 1995; Reggiani et al. 2002; Christianou and Ebenman 2005).

The ability of an ecosystem to maintain its self-organization and integrity, without undergoing the evolving, and possibly irreversible, change is associated with crossing the thresholds between stability domains. This notion is closely linked to the guarantee of the variety of ecosystem functions (De Leo and Levin 1997; Turner et al. 1998). Ecosystem functions, including interconnections between hydrological and geomorphological systems, photosynthesis and food web support, are the result of interactions between its structure and processes. Ecosystem structure refers to the tangible biotic and abiotic items such as plants, animals, soil, air and water of which an ecosystem is composed. Ecosystem processes refer instead to the dynamics of transformation of matter or energy between living and abiotic systems. These processes, in turn, are responsible for the provision of life support services, e.g. resilience benefits, such as assimilation of pollutants, cycling of nutrients, soil generation and preservation, pollination of crops, and maintenance of the balance of gases in the air (Maltby et al. 1996a, b). Furthermore, they also enable the development and

maintenance of the ecosystem structure that is, in turn, the basis for the continued provision of goods and services.

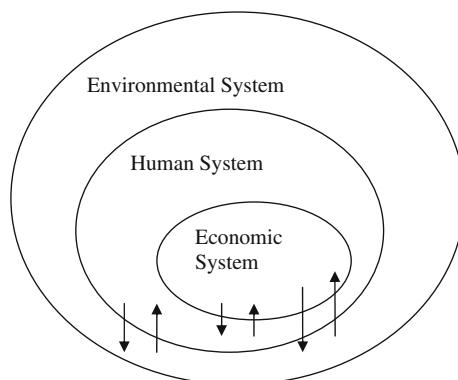
Natural and human systems coexist and are mutually interrelated. Arrows in Fig. 2 show the different interactions existing among them.

Humans share with other species a fixed amount of natural resources. If economic activities depend on the flow of goods and services provided by ecosystems, ecosystems are in turn dependent on the economy, due to the complexity of the interconnections between human and natural systems. Shocks to the joint economic–environment system (fires, storms or pest outbreaks) can affect both ecological and economic levels. This relationship will be discussed in more detail in the following sub-section.

Linking system's resilience to anthropogenic behaviour

A dominant element in recent discussions about ecosystem functioning is the worry about the influence of human activities in threatening the stability and continuity of ecosystems (Pimm et al. 1995; Simon and Wildavsky 1995). In recent years, many economists have focused their attention towards the valuation of the stability and continuity of ecosystems in terms of their ability to guarantee the provision of goods and services to mankind. Stability and continuity of ecosystems, i.e. resilience, today represents, more than ever, a valuable natural resource and requires our attention for two main reasons. First, it provides a wide range of direct and indirect benefits to mankind, which occur on both local and global scales. Such benefits include, *inter alia*, the maintenance of the genetic library, the direct provision of food, watershed protection and waste assimilation (Folke et al. 1996). Second, many human activities contribute to general, unprecedented pressures on natural systems and on their capacity to absorb exogenous perturbations without changes, i.e. their resilience. For instance, the accumulation of nutrient concentrations in lakes until a certain critical threshold is passed induces an increase in water turbidity and eutrophication (Deutsch et al. 2002). The consequent loss of animals and plants would affect recreation and fishing activities. Similarly, fire and grazing pressures for sheep and cattle production on rangelands produce a shift from grass to the less productive woody plant (small trees and shrubs) dominance (Deutsch et al. 2002). Overharvesting of fish stocks, global warming and pollution are some of the principal causes of coral reef degradation into alternative ecosystem regimes, dominated by macroalgae or sea urchins (Nordemar and Kautsky 2002).

Fig. 2 Linkages between system's resilience and anthropogenic behaviour.
Source: Batabyal et al. (2003), adapted



Humans are responsible for pressures on resilience at both species diversity and ecosystem functioning levels. At species diversity level, the assumption of a stabilizing role of keystone species implies that systems are more resilient and thus more able to absorb exogenous perturbations without changes. Such thresholds are the focus of many policy actions. The general idea is to respect the existence of extinction thresholds, even if accepting a certain degree of redundancy in the role of the different species. These, in turn, will insure against any unpredictable impacts in terms of deterioration of ecosystem processes and functioning (Mooney et al. 1995). In such a context, the level of human activities can induce ecosystems to cross such thresholds, threatening a system's resilience—including the overexploitation of species for commercial use. This is for instance the case, *inter alia* of Asian and African elephants, rhinoceroses and certain kinds of orchids and cacti, included among species protected by the Convention of International Trade in Endangered Species of Wild Fauna and Flora (OECD 1997).

At ecosystem functioning level, disturbances induced by human activities may threaten the ecosystem's ability to provide a wide range of services, including provisioning, regulating and cultural services directly affecting people and supporting services needed to maintain other services. Table 1 suggests a detailed list of such benefits.

For any ecosystem to function, a minimum level of variety of communities of living organisms and their abiotic environments is required. The task of evaluating an ecosystem's benefits for humans requires significant information regarding what the ecosystem does, what is needed for resilience and what its impact is on human welfare. The value of ecosystem structure is generally more easily appreciated than that of ecosystem resilience, due to the informational requirements necessary for the second to be known. Assessing ecosystem capacity to guarantee the provision of current nutrient retention and pollution absorption for any given region, for example, is extremely difficult. Such processes cannot in fact be easily observed and controlled by humans, who can only notice some effects of their malfunctioning. But ecosystem structure is also incompletely known. To assess the value of, for instance, the insect fauna diversity when many of these species have never even been described taxonomically, pushes human knowledge beyond its current limits (Westman 1985). Even if ecology has come to understand ecosystem processes to the extent that some relationships and their implications for humans are now evident, many questions still remain unsolved. However, due to the uncertain and potentially irreversible consequences in terms of ecosystem functioning and human welfare, the complex interplay between the range of human activities and the natural environment cannot be ignored. In particular, scientists face the important challenge of improving their understanding of the impact of resilience on human welfare: the preservation of ecosystem processes and their consequent good functioning requires in fact the preservation of ecosystem resilience.

Motivations for economic valuation

Introduction

Because we live in a world with scarce resources, one is frequently asked to make choices regarding the use and management of these resources. In this context, if policy makers decide to invest in the protection of, for example, marine ecosystems

Table 1 Ecosystem services

| |
|-----------------------------------------------------------------------------------------|
| <i>Provisioning services</i> |
| Food (crops, livestock, capture fisheries, aquaculture, wild plant and animal products) |
| Fiber (timber, cotton, hemp, silk, wood fuel) |
| Fuel, wood |
| Genetic resources |
| Biochemicals, natural medicines, pharmaceuticals |
| Ornamental resources |
| Fresh water |
| <i>Regulating services</i> |
| Air quality regulation |
| Climate regulation (global, regional and local) |
| Water regulation |
| Erosion regulation |
| Water purification and waste treatment |
| Disease regulation |
| Pest regulation |
| Pollination |
| Natural hazard regulation |
| <i>Cultural services</i> |
| Cultural diversity |
| Spiritual and religious values |
| Knowledge systems |
| Educational values |
| Inspiration |
| Aesthetic values |
| Social relations |
| Sense of place |
| Cultural heritage values |
| Recreation and ecotourism |
| <i>Supporting services</i> |
| Soil formation |
| Photosynthesis |
| Primary production |
| Nutrient cycling |
| Water cycling |

Source: Millennium Ecosystem Assessment ([2005](#)), adapted

integrity by creating a marine wilderness area, less financial resources would be available for other policy areas, such as national health. In addition, an investment in the protection of marine ecosystems' resilience brings along with it the provision of public values, which are not fully priced on current markets. In other words, marine ecosystems provide a wide range of benefits to humans and most are not valued on market prices. For example, a good functioning of marine ecosystems is able to provide an important role in balancing the local chemical composition of the water and we do not observe a market price that reflects the welfare impact of such benefit. Given that most human activities are priced in one way or other, in some decision contexts, the temptation exists to downplay or ignore marine ecosystem quality benefits on the basis of non-existence of prices. The simple and simplistic idea here is that a lack of prices is identical to a lack of values. Clearly, this is a biased perspective. Therefore, carrying out proper pricing is one of the main reasons to undertake economic assessment of environmental resources. Three other main reasons can also be identified: performing cost-benefit analysis; environmental accounting; and assessing natural resource damage. These will subsequently be considered in more detail.

Cost-benefit analysis

Cost-benefit analysis (CBA) is a welfare-theoretic method to trade-off the advantageous and disadvantageous effects of a proposed project by measuring them in monetary terms. CBA emerged as an attempt to systematically incorporate economic information that can be applied to project and policy evaluations. Since CBA has traditionally been defined in terms of gains and losses to society, project-oriented CBA has tended to be confined to public sector investment projects. The first evaluation studies were carried out in the USA in the 1950s to deal with ‘intangibles’ in a consistent way, e.g., for river basin projects and infrastructure projects. These methods found much application, *inter alia*, in World Bank practices. They were also heavily criticized for many inherent shortcomings, which has led to many new or adjusted methods, such as cost-effectiveness analysis, goals-achievement methods and multicriteria analysis (see Nijkamp et al. 1991).

The use of CBA to evaluate policy is more recent (see for an overview Boardman et al. 2000). Like an investment project, policies have costs and benefits. For example, standards for marine pollutant concentrations and taxation of marine pollutants are two different policies, which, in turn, are associated with different gains and losses to society. The basic rule of CBA in decision-making is to approve any potentially worthwhile policy if the benefits of the policy exceed the costs. Moreover, to make the best choice, a decision-maker should opt for the policy option with the greatest positive net present value. Other criteria exist, such as ranking and evaluating projects according to their ‘internal rate of return’ or according to the ‘benefit cost ratio’—see Hanley and Spash (1993) for a literature review on CBA and its application to environmental issues and Lima e Santos (2001) for the evaluation of biodiversity policy.

From an environmental agenda perspective, CBA has been used in the USA for evaluating policies since the late 1970s. However, only after President Ronald Reagan’s Executive Order 12291, in 1981, has CBA been extensively used for evaluating new regulations. In contrast, in Europe there are no legal requirements for CBA for new regulations, except in the UK, whose 1995 Environment Act envisions the use of CBA in policymaking. Clearly, the use and the critical judgments of CBA in public policy is still a matter of ongoing debate among most of the European policy makers.

Environmental accounting

Various efforts have been made to adjust national accounting systems and associated gross national product (GNP) statistics for the depreciation of environmental assets and for negative externalities such as pollution and the loss of biodiversity. The theoretical literature explores alternative ways of adjusting conventional estimates of national income to reflect environmental deterioration (Aronsson et al. 1997). Green (or environmental) accounting is one possible strategy.

The underlying idea is to add to the traditional national accounting system information on physical flows and stocks of environmental goods and services—the so-called physical satellite accounts. In the Dutch context, for example, the Netherlands Central Bureau for Statistics developed the NAMEA, a National

Accounting Matrix that includes both economic and Environmental Accounts (Keuning and de Haan 1996). An important aim of green accounting is to obtain an adjusted ‘green’ GNP. This can play a potentially crucial role in policymaking since the GNP has a powerful influence on macro-economic policy, financial markets and international institutions (OECD, IMF, and World Bank). If national income is wrongly estimated, then economic analysis and policy formulation are based on the wrong premises, thus ‘steering’ the society by the wrong compass (Hueting 1980; El Serafy 1999). Adjustment of the national accounts to reflect ecosystem quality loss will lower the GNP (Gerlagh et al. 2002). Nevertheless, practice shows that the adjustment of national accounting systems is not an easy task. It is therefore necessary to achieve international agreement about harmonizing GNP adjustments, allowing for the comparison of GNP and national accounts between countries. Independent of which valuation methods are used for this purpose, it is clear that monetary valuation of the depreciation of environmental assets and negative externalities, such as pollution and the loss of biodiversity, is a key element in green environmental accounting.

Natural resource damage assessment and legal claims

Natural resource damage assessments (NRDAs) appraise how much society values measures to avoid the destruction of natural resources. An important benchmark in the history of NRDA is the massive oil spill due to the grounding of the oil tanker Exxon Valdez in Prince William Sound, in the northern part of the Gulf of Alaska, on March 24, 1989. This was the largest oil spill from a tanker in USA history. More than 1,300 km of coastline were affected and almost 23,000 birds were killed (Carson et al. 1992). After the oil spill, the State of Alaska commissioned a legal action in order to assess Exxon’s financial liability in the damage to the natural resources. A national contingent valuation study estimated the loss to USA citizens as a result of the oil spill, estimated at \$2.8 billion. For the first time, a governmental decision expressed the legitimacy of nonuse values as a component of the total damage value. To date, NRDAs are only undertaken in the USA and have not yet become an issue in the European policy agenda because of different legal arrangements between member states. The recent sinking of the tanker Prestige along the Galician coast makes this aim very significant.

Such sinking caused in November 2002 was probably the largest European oil spill to date, with about 60,000 tons of heavy fuel oil leaked into the sea and affecting more than a thousand km of coastline (Cajaraville et al. 2005). The Spanish Ministry of Science and Technology launched in 2003 two special actions, one of which aimed to monitor the health of sentinel coastal organisms and the other focused on determining the effects of the oil spill on the platform ecosystems and fisheries resources. The second action included also the analysis of the socioeconomic effects of the oil spill: the Economy of Fisheries Resources group of the University of the Basque Country was charged with assessing the losses in the fish-extraction, commercial and transformation sectors in Basque Country. The evaluation of the losses focused on some socioeconomic variables of interest for the whole sea-industry complex, including income and employment levels, but no NRDAs were undertaken.

Resilience as a source of economic value

Introduction

As we have seen, the concept of resilience was put forward in the field of natural sciences. In their study, economists are concerned with the magnitude of disturbance that can be absorbed before an ecosystem is displaced from one state to another. In other words, with the ability of an ecosystem to maintain its self-organization without undergoing the destructive and possibly irreversible change involved in crossing the threshold between stability domains (Pearce et al. 1989; Deutsch et al. 2002). The maintenance of system self-organization is interpreted in terms of the ecosystem's stability and integrity of the platform that, in turn, is responsible for the provision of a wide range of direct and indirect benefits affecting human welfare. In short, from the economic perspective, the relevance of resilience is mainly due to its role in guaranteeing the provision of a wide range of benefits, including the ecosystem absorption capacity of external perturbations. Resilience represents a valuable natural resource in particular today, in a worldwide context characterized by general, unprecedented human pressures on the natural environment and the consequent increasing threats to ecosystems' stability and integrity.

One can question why, if resilience generates so many benefits for humans it has been ignored for so long by the policy agenda and it is still ignored today when, more than ever, we put unprecedented pressures on ecosystem stability. When answering this question, it is current practice to distinguish between 'proximate' and 'fundamental' factors that underpin the ecosystem's ability to buffer against disturbances. While the proximate factors relate to the worldwide trend of human population growth, and its impact on production and consumption patterns, the fundamental causes are associated with the conditions within which system resilience decisions are made. Two important fundamental causes emerge (Nunes et al. 2003). The first relates to market failures and the second to the lack of property rights. Many resilience benefits, such as the ability to maintain the genetic library, are not 'cashed' flows, i.e., there is no market price mechanism that fully captures such benefits. In other words, markets fail to internalize protection benefits. For this reason, these are known in the economic literature as positive external effects (or externalities), i.e., positive effects outside the market on the welfare or productivity of other individuals. In such a context, the individual rate of return on conservation will almost certainly fail to compete with the individual rate of return on development projects. This is a consequence of the individual utility maximizing behaviour, ignoring the existence of externalities. According to the usual economic analysis, the optimal individual choice corresponds to a preservation of resilience below the level that would be socially optimal, because the external effects are not included within the individual rational calculation.

The second fundamental cause is related to the lack of property rights. The unrestricted depletion of ecosystem resilience due to the lack of enforceable property rights causes negative externalities to society, because there is no owner able to privately capture resilience benefits. This identifies an example of what is usually called, since the seminal work of Hardin (1968), 'the tragedy of the commons'. In a context in which individuals are supposed to be rational, the personal calculation of utility would induce everyone to compare his share of the cost of decreasing

resilience to his share of the cost of preserving resilience. Since for each individual the first one is less than the second one due to the absence of property rights, the result will be a loss of ecosystems' resilience greater than the socially optimal level. In particular, population growth makes today the problem of properly defining property rights even more relevant. At worldwide level, this problem emerges also because of the high importance of the spatial element arising from a reciprocal relationship: (1) local, anthropogenic rooted processes have global impacts in terms of system resilience; and (2) global trends in system resilience give rise to local effects. For example, natural habitats have been historically converted to agricultural use. Such process has heavily affected ecosystem functioning and structure and, by reducing ecosystems' resilience, has affected geochemical cycles and thus contributed to the global warming we are now experiencing. The global climate change, in turn, is having local consequences in terms of soil erosion, downstream sedimentation, flooding and salinization.

Resilience as a source of welfare

Demographic, social, cultural and economic trends have many impacts on the functioning of both natural and human systems. A reduction in the systems' resilience makes them more vulnerable to external perturbations, which otherwise would have been absorbed without structural change (Folke et al. 1996). An emblematic example of loss of resilience is represented by the construction of the Aswan dam that, by ending the annual floods of the Nile river, has impoverished Egyptian agriculture and induced a great portion of the rural population to migrate into Cairo. This in turn was responsible for additional welfare damages in terms of urban poverty and unemployment (Batabyal et al. 2003). Another significant example is captured in the mid-western regions of the United States of America. There, the loss of flood protection services provided by upstream wetlands as a consequence of land use decisions has played a key role in the intensive flooding of Mississippi river and its tributaries (Batabyal et al. 2003).

The reduction of systems' resilience, measured by an overcoming of ecological thresholds, causes discontinuities in the provision of ecological service flows, and a negative impact on human welfare. This situation configures a challenge for the economic theory because of the uncertainty of the thresholds' levels values and the magnitude of the change (Muradian 2001). In the case of the greenhouse gas emissions, for example, marginal increases in carbon dioxide emissions lead to marginal increases in global temperature, but when a critical threshold is crossed the consequent massive warming can induce important destabilizing phenomena, such as *El Nino* and *La Nina* events (Batabyal et al. 2003).

In case of irreversible damages or slowly reversible changes, welfare costs derived from the reduction of system resilience are imposed on both present and future generations (Perrings and Stern 1999). Irreversibility, in fact, typically occurs when the ecosystem original state, and the consequent flow of goods and services to humans, can be restored only at excessive costs to society, either in terms of resources allocation or of time required (Van Kooten and Bulte 2000). In both cases, the welfare costs associated to irreversible environmental damages are not easy to quantify. From one hand, it is not always possible for scientists to ex ante assess their amount, due to the limited knowledge on the type and duration of the complex natural phenomenon involved. On the other hand, uncertainty also derives from the

lack of knowledge on the preferences of future generations: different welfare priorities could imply different environmental concerns. In this context, resilience can then be interpreted in terms of *natural insurance capital* (Prakash and Pearce 1993; Barbier et al. 1994; Folke et al. 1996; Deutsch et al. 2002). Therefore, any decrease in the level of uncertainty is characterized and measured in terms of an increase in the supply of insurance against potential transformation of natural capital. Such an insurance effect is stronger the weaker is the substitutability between environmental capital and human-made capital (e.g. technology). Resilience, at least for some forms of environmental capital with limited substitutability, represents then a *critical capital* (Prakash and Pearce 1993), captured in terms of both environmental functions for the human system (ecosystem goods and services) and environmental functions for the natural system (life-support functions) (Deutsch et al. 2002). The loss of resilience, by altering essential ecosystems' functions and processes, modifies the risk associated with a given set of environmental conditions and induces a different value of potential productivity, in terms of flows of goods and services (Brock et al. 2000). The task is now to evaluate the benefits of ecosystem resilience for human welfare. However, we first need to present and discuss the underlying characteristics that the economic valuation perspective relies upon.

Economic valuation perspective

The valuation of any scarce resource, such as ecosystem resilience, relies on cultural, political and religious determinants. As proposed by van Ierland et al. (1998), the perspectives on value vary according to the underlying human attitudes with respect to natural environment. For the sake of illustration, we here take into account two opposite perspectives, the eco-centric value perspective well known in the literature as *deep ecologist* and the anthropocentric *techno-economic dominance* (Table 2).

According to the *deep ecologist* value perspective, top priority is given to the conservation of the environment, in general, and protection of resilience, in particular, independently of their importance in terms of their role in the human economic activities. The underlying idea of this biotic, egalitarianism anchored perspective, is that nature is characterized by intrinsic values (Ehrenfeld 1988). On the contrary, the *techno-economic dominance* value perspective assumes a rather optimistic view with respect to the self-regulation capacity of the environment and accepts depletion in natural resources to reach economic growth targets, without recognizing any intrinsic right for protection. In between, the other attitudes (*ecological approach*, *stewardship*, *multipurpose use*, *economic attitude*) differ from each other because of a decreasing relevance attributed to the environment and an increasing relevance attributed to economic activities.

Table 2 A classification of attitudes towards nature

| Attitudes | Principles |
|---------------------------|------------------------------------------------------|
| Deep ecologist | Only biodiversity issues matter |
| Ecological approach | Recognition of economic needs |
| Stewardship | Protect biodiversity, but allow economic activity |
| Multipurpose use | Biodiversity and economic activity |
| Economic attitude | Priority to economic activity |
| Techno-economic dominance | Only economic issues matter |

Source: van Ierland et al. (1998), adapted

The present paper explores an economic perspective with respect to the valuation of ecosystem resilience. For the relevance given to the preservation of the environment and to the practice of economic activities, this economic perspective is placed between the above mentioned multifunctional use and economic attitude. In particular, following the framework proposed by Nunes and van den Bergh (2001), such perspective is based on an *anthropocentric* point of view on value. This means that the concept of value has its foundations in individual welfare. The basic premise of economic valuation, and thus economic value of a resource, is the effect of the supply of the same resource on the well-being of the individuals who make up the society. Therefore, if society wishes to make the most in terms of individuals' well-being maximisation, the issue of the assessment of the total economic value of resilience benefits is a key issue in terms of policy decisions. Implicitly, this also means that the economic perspective on resilience value embraces an *instrumental* approach. This makes explicit the fact that resilience benefits are used for instrumental purposes, either in terms of production opportunities or in terms of consumption opportunities (Fromm 2000).

Many people, however, do not feel comfortable with placing an instrumental value on natural resources, in general, and resilience, in particular. The common argument is that the resource has a value on its own—also known as ‘intrinsic value’. An extreme version of this argument claims that instrumental monetary valuation is a nonsense exercise (Ehrenfeld 1988). This approach is not embraced here. On the contrary, the *instrumental* approach is based on the idea that making public or private decisions, which affect system resilience, implicitly means attaching a value to it, which is disclosed in terms of different changes in the level of resilience benefits associated to each scenario or policy options. In other words, humans have preferences with respect to different states of the world and their environmental quality characteristics, and value changes (rather than levels) of environmental quality characteristics (including system's resilience), which are relevant for their welfare.

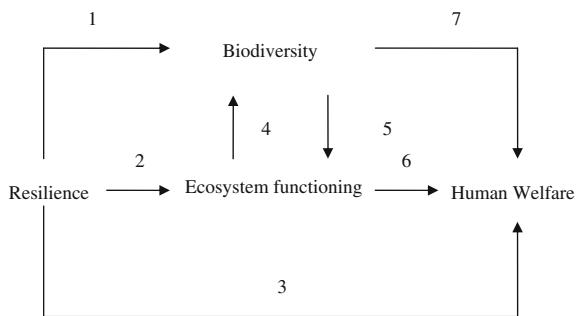
Furthermore, the economic perspective on the valuation of ecosystem resilience is a monetary valuation. Monetary indicators serve as means and not as ends in valuation. In short, economists make the use of monetary indicators as common units for the comparison and ranking of alternative resilience scenarios or policy options. The magnitude of the monetary indicator translates the value of the resilience benefits in human welfare, in terms either of the individual production or consumption opportunities. Since monetary valuation reflect individual preferences and all individuals are invited to participate in the valuation, it can be said to be rooted in a democratic approach allowing direct comparisons with alternative options in order to make public decisions, including those affecting ecosystem resilience.

Finally, the economic valuation is anchored in a *reductionist* perspective and for this reason is based on the idea that one is able to disentangle, or disaggregate, the total value of resilience benefits into different economic value categories, notably direct use and passive use or nonuse values (Pearce and Moran 1994), reflecting the different human motivations (*bottom up approach*, Nunes and van den Bergh, 2001). The next section will focus on these different economic value categories.

A possible classification of resilience's value components

Bearing in mind the proposed economic valuation approach, the different value categories of resilience can be identified and described by referring to a simple conceptual framework as shown in Fig. 3.

Fig. 3 Resilience's value components



A first value category of resilience is denoted by link 1–7. This captures the benefits humans derive from the maintenance of ecosystem stability, expressed in terms of the intertemporal provision of goods and services. This resilience value component is referred to as *direct use value* and captures both the value of the information pool contained in plants and animals (including genetic diversity) as well as the value of the supply of a variety of landscapes, habitats and respective biotic communities (including ecosystem diversity). As far as the impacts of resilience on gene diversity are concerned, one can proceed in assessing this value component in terms of its added value as an input in the provision of market priced goods (such as new medicines or pharmaceutical products). Alternatively, the impacts of resilience on ecosystem diversity can be inferred by individual demand on natural habitats, including experience and recreational values.

A second value category of resilience is captured by link 2–6. This denotes the benefits accruing to humans by ecosystem functioning, expressed in terms of its ability to buffer against disturbances. This resilience value component is referred to as *indirect use value*. This value component includes the welfare that humans derive from preventing any malfunctioning in the ecosystem and thus avoiding any interruption in the provision of environmental and ecological services, such as flood control, groundwater recharge, nutrient removal, toxic retention and CO₂ sequestration.

Another value category of resilience is captured by link 3. This denotes the benefits accruing to humans from ecosystem stability, and its impact in terms of the guarantee in the intertemporal provision of goods and services, and ecosystem integrity, expressed in terms of its impact in guaranteeing the intertemporal ability to buffer against disturbances, even if none of the both are directly consumed or experienced by the individual. In other words, it simply corresponds to individual knowledge that these resilience benefits exist, independently of their human use. In general terms, these reflect moral and philanthropic considerations, including intra and inter generations altruistic motives. For this reason, link 3 denotes a *passive or non-use value component* of resilience.

In addition, we have a value category captured by link 4–5. This depicts the feedbacks that human experience and knowledge of resilience benefits cause on ecosystem stability and integrity. In other words, this value category is interpreted as an insurance against potential damages caused by the feedback of the wide range of human activities on ecosystem stability and integrity. For this reason, link 4–5 denotes a *option value component* of resilience. Next sub-section will focus on the

analysis of this value component of resilience, by looking in particular at its policy implications in terms of natural disaster prevention and management.

The option value component of resilience: policy implications

As previously stressed, resilience derives part of its economic value from its role in protecting against potential damages due to a loss of ecosystem stability and integrity (option value component). From this point of view, resilience corresponds to a measure of ecosystems' *vulnerability* to damage, defined as the probability that ecosystems are affected by a certain risk factor (Cardona 2003). As such, resilience identifies a key element in risk and natural disaster prevention and management. In fact, a reduced vulnerability implies a reduction in risk and consequently in the probability of future natural disasters. Then, the analysis of the main issues on risk assessment from the perspective of disaster risk may help in defining the option value component of resilience.

Following Cardona (2003) and Freeman et al. (2003), it is possible to divide the different components of disaster risk management into two phases. Actions required in the pre-disaster phase include risk identification, risk reduction and risk transfer, while the post-disaster phase is primarily devoted to disaster management actions. *Risk identification* deals with hazard assessment, monitoring and forecasting, as well as with vulnerability and risk assessment. *Risk reduction* refers instead to preventive and mitigation policy measures, aimed to intervene on the causal factors of the negative event. *Risk transfer* includes insurance and financial protection through specific instruments, such as national or local calamity funds, catastrophe bonds, public services with safety regulation (energy, water and transportation). Once the negative event has occurred, *disaster management* identifies response and recovery actions devoted to humanitarian assistance, damage assessment, rehabilitation and reconstruction of damaged infrastructure, revitalization of affected sectors.

Within this framework, resilience plays a significant role during the pre-disaster phase as insurance against the uncertain and potentially irreversible effects of ecosystem malfunctioning, i.e. as factor reducing risk. In particular, resilience acts as a factor reducing the expected total damage related to the negative event, at both prevention and mitigation level. As such, its option value component can be approximated by two different components: by the costs of implementing *prevention* policy measures, i.e. policies aimed to reduce the probability of disaster; and by the costs of implementing *mitigation* policy measures, i.e. policies aimed to ex ante reduce the economic losses due to the eventual occurrence of natural disasters or extreme events.

As recognized by the recent literature on disaster prevention and management (Rose 2004), the system's capacity to absorb the feedback of the wide range of human activities on ecosystem stability and integrity deals in particular with three main elements. These are: *reduced failure probability*, *reduced consequences from failure* and *reduced time to recovery*. The first element depends on how a community intervenes to reduce the probability of structural or system failure, for example by implementing public policies aimed to preserve system's resilience through limitations on agricultural practices near river basins. The second element results instead from ex ante protective measures aimed to minimize the negative effects due to structural or system failure, such as protective barriers in case of periodical flooding.

Finally, the last element refers to how quickly the system returns to normality in case of external shocks.

The following section will discuss an illustration on the economic value measurement of resilience benefits in terms of natural insurance against high water events in the city of Venice. Such benefits will be expressed in terms of the avoided welfare costs, which would be associated to the negative event of high water in case of low Lagoon system resilience. At this aim, the analysis will focus on welfare costs derived by business interruption. Even if among the welfare costs associated to natural disasters particular emphasis has traditionally been devoted to the measure of property damage, other categories of measurement are recently receiving significant attention (Perrings 1998; Rose 2004; Carraro and Nunes 2004). Then, the social value of maintaining the Venice Lagoon resilience will be approximated with the value of the forgone output from the human activities normally carried out in such ecosystem and interrupted because the disaster occurred.

The Venice Lagoon case study

Periodical flooding as a signal of ecosystem's resilience loss

The Venice Lagoon illustrates a particular type of ecosystem, in which natural and anthropogenic dynamics coexist, being strongly interlinked to each other: complex global transformation processes (e.g. climate change, sea level rising) are added to strong local human pressures (e.g. water pollution, solid waste).

Natural, historical and cultural specificities make the area of great interest for an economic analysis, in particular due to the effects of the growing anthropogenic pressures inducing dynamic disequilibria. A typical example of these disequilibria is the more and more recurrent phenomenon of *acqua alta*, i.e. the periodical high water events causing (partial) flooding of the historical centre of Venice. Venetians have learnt to coexist and deal with this sort of periodical event since the very beginning of the history of the city, by adapting their own behaviour to tackle this problem. Nevertheless, during recent decades the city has experienced a systematic increase in the intensity of the phenomenon, as confirmed by the upwards trend of mean tidal excursions in Venice. Figure 4 depicts the average water level trend from 1993 to 2001.

The high water impacts on architectural, artistic and cultural heritage and the economic damages to the population and its visitors are of increasing concern to both Venetians and policy makers (Ministero dei lavori pubblici 1997). The factors influencing such a pattern include, *inter alia*, the increase of the Adriatic sea level of about 23 cm during the twentieth century. This is due to both natural and human causes, among which particularly relevant are the subsidence of the islands of Venice and the global climate change phenomenon. Nevertheless, the increasing intensity and frequency of the high water event can be considered a signal of low resilience of the Lagoon ecosystem as a whole (Ministero dell'Ambiente 1998).

Most of the existing valuation studies analysing the economic impacts of high water events in the Lagoon refer to the introduction of the mobile-gates project called MOSE (*Modulo Sperimentale Elettromeccanico*) and usually quantify structural damages according to physical, non-monetary approaches.



Fig. 4 Intertemporal series of mean tidal in Venice. Source: <http://www.comune.venezia.it/maree/dal1867.asp>

In a recent valuation report, Carraro and Nunes (2004) propose instead a monetary assessment of the economic short-term impacts of high water events on all registered business activities located and operating in ground floor units in the city of Venice. As such, this assessment provides only a partial estimate of the negative impacts of high water, living aside other impacts, as for instance those on tourism earnings and cultural heritage. A short-term perspective means that the attention is focused only on the consequences of high water events for the business activities already in place, without extending the analysis also to the potential variation in the composition and number of such activities. Impacts are viewed as a sum of *on site damages* and *off site damages*. The first damage category refers to damages on the structures and materials due to the infiltration of water. The second damage category instead captures the damages attributable to the reduced overall functioning of the city dynamics during high water events. In particular, this category of damages is related to the uncertainty with respect to the future revenues of business activities and for this same reason impacts on the economic value of such activities.

Bearing in mind such a categorizing of acqua alta damages, the economic valuation of the first damage category can be approximated by the costs connected to the implementation of mitigation policy measures. These measures are aimed to minimize the damages high water and salinity cause to building elements through the adoption of high water protection measures and equipment, such as hydraulic pump, the rising of pavements and *paratia* (a system of mobile barriers protecting doors that give access to street). The costs related to mitigation policy measures then reflect a *private insurance* perspective, since they capture the value of the direct damages caused by high water on the architectonical structure and equipment (e.g., inner and front door maintenance, cleaning of pavements and maintenance of walls), which are financially supported by the privately owned business activities.

The economic valuation of off site damages is instead related to the costs of reducing the likelihood of flooding events through the implementation of prevention

policy measures. Such measures typically cannot be undertaken by private individuals, but has to be the result of concerted actions at regional, national or international scale. In fact, the off site damage component refers to a set of high water impacts that are not routinely traded in regular marketplaces. These include *inter alia* the impact of the high water, and respective uncertainty of the city dynamics' performance, on the economic value of the business activities. As a consequence, the economic valuation of off site damages is relevant from a *public protection* perspective.

Empirical valuation of on site damages

The empirical valuation is focused on the estimation of both on site and off site economic damages induced by the high water event. The estimation exercise referred to the first damage component is based on two COSES surveys (1999 and 2001). In order to proceed with the monetary assessment of damages, the high water events considered in the empirical exercise include the valuation of two possible high water events: single exceptional events and weakly periodical flooding episodes and general high water scenarios. In particular, three different scenarios are taken into account in addition to the current situation ('business as usual' scenario), which reflects the historical annual average frequencies of high water events registered by the Venetian Municipality during the period 1996–2001. The first scenario ('Defence 110') corresponds to the situation in which collective defensive measures are taken against all events above 110 cm. The second scenario ('Climate change') considers an average sea-level rise of 10 cm induced by climate change events. Finally, the third scenario is a combination of the 'Defence 100' and 'Climate change' scenarios.

This part of the valuation exercise combines an integrated dose-response modelling with an expert-based valuation approach, relative to maintenance and repair activities due to high water and related market prices: it assesses the physical damage on structures and materials and estimates the economic value of the damage without retrieving people's preferences.

The estimation results, referred to the considered different scenarios, are shown in Table 3. As can be noticed, the total on site economic damages range on average between 4.4 and 2.4 millions of Euro. In particular, if the climate change hypothesis is assumed, the estimated increase of on site damages is around the 43% with respect to current situation. The introduction of a public protection project induces a reduction in the estimated total on-site economic damages equal to the 27% with respect to current situation. When the climate change hypothesis is assumed, the estimations reduction due to the public protection project is instead equal to the 40%.

This resulting estimates provide just a partial proxy for the total on site damages, because they do not include the economic value of impacts on furniture, working hours and commodities. As such, they only partially capture the economic value of the privately implemented mitigation policy measures.

The second part of the valuation exercise is based on a survey instrument portrayed in terms of conjoint valuation method (Carraro and Nunes 2004), since the monetary valuation of off site economic damages refers to a damage component not fully captured by market prices. This type of survey based valuation methodology, applied to a CORILA questionnaire (2003), is characterized by the use of a specific

Table 3 On-site economic damages

| | BAU | Climate change | Public protection project + 110 cm | Public protection project + 110 cm and climate change scenario |
|----------------------------------------------|---------|----------------|------------------------------------|----------------------------------------------------------------|
| <i>Cost category</i> | | | | |
| <i>Substitution of inner doors</i> | | | | |
| Higher bound | 1441144 | 2233543 | 460253 | 460253 |
| Lower bound | 893049 | 1638794 | 402604 | 460253 |
| <i>Maintenance of front doors</i> | | | | |
| Higher bound | 135281 | 284389 | 108467 | 124133 |
| Lower bound | 63598 | 164415 | 63598 | 122566 |
| <i>Maintenance and cleaning of pavements</i> | | | | |
| Higher bound | 78797 | 188408 | 42151 | 100401 |
| Lower bound | 68519 | 163833 | 36653 | 87305 |
| <i>Maintenance of walls</i> | | | | |
| Higher bound | 2920301 | 3232043 | 2773044 | 3019921 |
| Lower bound | 1240247 | 156812 | 1106891 | 1380724 |
| <i>Total on-site economic damages</i> | | | | |
| Higher bound | 4575522 | 5938383 | 3383916 | 3704709 |
| Lower bound | 2265413 | 3535853 | 1609746 | 2050849 |

Source: Breil et al. (2005), adapted

econometric model, which is anchored in the random utility micro-economic framework, exploring the direct impact of different high water levels on the choice of the business activities. Respondents choose between alternative scenarios according to respective impact in terms of welfare gain/loss. Bearing in mind the respondent's choices, it is possible to infer such impact in monetary terms, reporting this magnitude as a proxy of the economic value of the business activity. The aim is, *inter alia*, to quantify the negative impacts of high water in terms of its limiting public access and usability of the city and its business activity.

This specific methodology has been conceived so as to: (1) identify a set of characteristics that together with the effects of high water influence the economic value of a business activity located at ground level in the city of Venice; (2) employ a valuation tool that links the economic value of a business activity with a consumer choice model and (3) estimate the impact of the different characteristics under consideration in the individual choices, thereby inferring the respective valuation mechanisms in monetary terms.

Bearing in mind this economic valuation framework, a bid valuation function for alternative sets of business locations is estimated, assessing the marginal impact of the different characteristics under consideration. In particular, one business activity is modelled and described with respect to the following three different characteristics: the position of the business activity with respect to the sea level; whether the shop is accessible by means of a catwalk; whether the shop is located in an area mainly visited by tourists.

All the estimation results are summarized in Table 4. The monetary assessment of damages induced by an exceptional flooding event, such as the extraordinary flooding of 16th November 2002, is estimated at 10.6 millions of Euro, while the economic value of damages of a year similar to 2002 is estimated at 30 millions of Euro. The total economic value of damages due to high water event for an entire year are estimated at 22 millions of Euro.

Table 4 Estimation results

| | | |
|-----------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------|
| <i>Source:</i> Carraro and Nunes (2004) | On site damages per year Costs due to an exceptional event (16 november 2002) On site costs of a year similar to 2002 (including protection measures) Total on site and off site damages per year (CORILA questionnaire) | 2.4–4.4 millions Euro 10.6 millions Euro 30 millions Euro 22 millions Euro |
|-----------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------|

Conclusions

This paper has focused on the analysis of ecosystem resilience as a scarce environmental resource. The attention has been directed on resilience value from an economic perspective, exploring the motivations for economic valuation and its relevance in terms of human welfare. In this context, resilience has been interpreted as a natural insurance capital against the risk of ecosystem malfunctioning and the consequent damages associated to a potential interruption of the ecosystems' ability to provide goods and services to humans. From the analysis two main important messages have emerged.

The first message is of a methodological nature and refers to the review of the main reasons that steer economists to be interested in studying resilience, as the concept has been originally developed in the field of natural sciences. The economic perspective has been put forward in order to shed light on the basic premises that anchor the economic valuation of any scarce resource, such as resilience and its benefits. It has been argued that policy guidance constitutes an important motivation for pursuing economic valuation of resilience since respective monetary estimate is crucial when performing a cost-benefit analysis, natural resource damage assessment or green environmental accounting. Moreover, given that most of the human activities are priced in one way or another and most ecosystem stability and integrity benefits are not market priced, one can be tempted to downplay or ignore resilience benefits on the basis of non-existent prices. The simple and simplistic idea here is that a lack of prices, basically induced by market failures (externalities and public goods) and the lack of enforceable property rights, is identical to a lack of values. Clearly, this is a biased perspective. The need for carrying out proper pricing is instead one of the main reasons to undertake economic assessment of environmental resources, such as resilience. In this context, we developed a simple framework to identify and describe the different value components related to resilience which economists need to assess when performing an economic valuation exercise.

The second message emerges from the empirical exercise briefly discussed at the end of the paper, on the economic assessment of damages induced by high water events in the city of Venice. The increasing frequency and intensity of flooding, causing many serious damages to business activities carried out at ground level, can be interpreted as a signal of a decreasing resilience in the natural Lagoon system. Bearing in mind such a premise, the analysis has focused on the interpretation of the estimation results in terms of the economic value of the Lagoon resilience. In doing so, we referred to both a private insurance perspective and a public policy perspective. From the first perspective, the economic value individuals attribute to resilience because of its contribution to the reduction of the negative impacts of flooding on business activities can be approximated by the prevention and mitigation costs necessary to minimize the welfare losses. In particular, such costs correspond to

the amount individuals are willing to pay for ex ante limiting the damages caused by flooding on business activities. From the public policy perspective, the estimate of the off-site damages reflects the uncertainty with respect to the future revenues of the business activities. Taken together, the estimated on site and off site damages can be considered as a proxy of the option value component of the total economic value of the Lagoon system's resilience. In fact, by assuming that the higher frequency of flooding is a signal of a progressive loss of resilience in the Lagoon, then the higher the resilience, the lower the frequency and intensity of high water events (resilience as natural insurance capital). Investing in measures to minimize the welfare losses due to flooding on business activities (i.e. paying for mitigation and remediation costs) can be considered as an insurance premium against the economic damages induced by high water, i.e. the costs to reduce the risk of negative consequences related to this event. In other words, for individuals working in the business activities located at the ground floor of some Venetian buildings the costs of reducing the economic damages of flooding can be considered as a proxy of the economic value of the possibility to maintain as much as possible constant business output flows in the future. Such costs represent then the amount individuals are willing to pay to both reduce impacts from ecosystem failure (high water events) and reduce time to recovery from the negative consequences of the failure.

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Natural oak forest vs. ancient pine plantations: lizard microhabitat use may explain the effects of ancient reforestation on distribution and conservation of Iberian lizards

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Abstract. Natural vegetation in Europe appears nowadays deeply modified by human activities. In the Guadarrama Mountains (Central Spain), ancient reforestation with Scots pines, *Pinus sylvestris*, replaced original deciduous pyrenean oak, *Quercus pyrenaica*, forests (since the Roman period). However, the effect of reforestation on fauna remains little known, especially in reptiles. We described patterns of microhabitat selection in several species of Lacertid lizards, and analyzed whether the modification of the original vegetation affected distribution and population densities of lizards. The species of lacertid lizards found in oak forests (*Psammodromus algirus*, *Lacerta lepida* and *Podarcis hispanica*) were different to those of in pine plantations (*Podarcis muralis* and *Podarcis hispanica*). Lizards did not use habitat at random and this could explain differences in species found in both forests, which differed in some microhabitat structure characteristics. Most lizards selected microhabitats with rocky outcrops, with low cover of trees, and close to refuges. These microhabitat preferences also explained abundance of lizards in transects. From the perspective of conservation and management of lizards, pine plantations seem not to contribute too much to the diversity of lizard species because species typical from oak forests were lost. This study has implications for pine reforestation management, because allowing the recolonization by under-story oaks, and leaving some open areas, without trees but with dense shrubs and rocks inside reforestation would contribute to maintain lizard populations.

Introduction

Natural vegetation in Europe has been deeply modified by human activities. Pine plantations extend over much of the Iberian Peninsula. Some have been planted in the last 50 years due to new agriculture policies, which aim to decrease food production and restore the environmental diversity previously lost through agricultural intensification (Díaz et al. 1998; Schmitz et al. 1998). However, plantations sometimes were made thousands of years ago to replace original oak forest with faster growing species used for lumber. For example,

the Guadarrama Mountains (Central Spain) are covered with two different types of natural forests: at low and intermediate altitude levels (1200–1700 m) natural vegetation is dominated by forests of deciduous Pyrenean oak, *Quercus pyrenaica*, whereas at high altitude (1700–1900 m) the natural vegetation consists of forests of Scots pine, *Pinus sylvestris* (Rivas-Martínez et al. 1987). Since ancient historical times, oak forests were used for production of charcoal and for extensive livestock grazing, whereas pine forests were traditionally managed for lumber exploitation. Oak forests were progressively deforested, but later reforested with pine plantations (Izco 1984). Thus, plantations of pines now extend over a wider altitudinal range of 1200–1900 m. Traditional pine reforestation dated from Roman period, S. I b.C. Subsequent pine reforestations have succeeded thought history. The natural pine forests are still present at high altitude, whereas the oak forest has been relegated to small areas. Pine plantations are now old enough so that they apparently resemble the natural pine forests found at high altitude. However, subarboreal and herbaceous vegetation associated with these old pine plantations are typical of that of the original oak forest, although diversity of annual herbs has decreased and vegetation structure has been modified (Izco 1984; Rivas-Martínez et al. 1987).

Evaluation of the effects of pine reforestation on animal communities has mainly focused on the effects of recent plantations on bird populations (Potti 1985; Carrascal and Tellería 1990; Díaz et al. 1998; Goldstein et al. 2003). The long-term effects of reforestation have been rarely studied, and there has been a general lack of studies focusing on other animal groups such as reptiles. However, in Mediterranean climates, reptiles are one of the more prominent groups of animals. The Iberian geographical area includes many endemic species with populations reaching higher densities than in Central Europe (Corbett 1989). Furthermore, lizards are important keys in the trophic chains of Mediterranean ecosystems (e.g., Martín and López 1996) and changes in their populations should affect other taxa, such as snakes, raptors or some mammals.

Numerous species of lizards show preferences for specific structural features of the habitat (Heatwole 1977; Martín and López 1998, 2002) that make them vulnerable to changes in the structure of vegetation. For example, their thermal requirements make them dependent on availability of sunny places for basking (Martín and López 2002; Scheers and Van Damme 2002; Sabo 2003). Also, dependence on habitat structure for refuges from predators can be an important determinant of lizard survival (Milne and Bull 2000; Webb and Shine 2000; Souter et al. 2003). Lower mobility and dispersal abilities of lizards, compared to birds or mammals, may also increase their vulnerability to local extinction to a greater extent than for other groups (Díaz et al. 2000; Mac Nally and Brown 2001). To understand how the fauna respond to these changes on vegetation, we can use models that relate the abundance of a species to variables describing the structure of the habitat. Models allow predictions to be made about a species' response to artificial and natural habitat

changes (Martín and López 2002). For Mediterranean lizards, some studies have identified their habitat requirements (e.g., Carrascal et al. 1989; Díaz and Carrascal 1991; Castilla and Bauwens 1992). However, the effects of habitat modification on lizard populations have not been extensively analysed in Europe (but see Santos and Tellería 1989; Díaz et al. 2000; Martín and López 2002).

In this study, we aim to analyse whether traditional and ancient conversion of oak forest to pine plantations have altered lizard community composition in the Guadarrama Mountains. In the case of reptiles, microhabitat diversity and structure has often been observed to be more important than macrohabitat structure (e.g., forest type) as a predictor of composition of lizard communities (Pianka 1967; Szaro and Belfit 1986; Menke 2003). Therefore, we expected that if microhabitat structure remained similar in pine plantations than in natural oak forests, lizard populations might have adapted to ancient changes in macrohabitat (i.e., from oak to pine forests) and, then, we may expect that the same lizard species were found in both the natural oak forests and the ancient pine plantations. In contrast, changes in microhabitat structure associated to changes in macrohabitat structure might have altered lizard community composition to resemble that of natural pine forests situated at higher altitude, thus, losing typical species of oak forests. We further analysed whether the number of lizards (i.e., relative abundance) of each species observed in each forest patch was dependent on modifications of the physical structure of the habitat.

Materials and methods

Study area

The study was conducted in the Guadarrama Mountains (Madrid province, Central Spain) at the altitudinal range of 1200–1600 m. In this area and altitudinal range, there is a Mediterranean climate with a mean annual temperature range of 8–12°C (Izco 1984), and the natural vegetation was originally dominated by Pyrenean oak, *Q. pyrenaica*, forests (Rivas-Martínez et al. 1987). However, the area is now mostly covered with ancient plantations (since Roman period, S.I b.J.) of Scots pine, *P. sylvestris*, whereas there are also some remains of the original oak forests in small concrete areas.

In this area, the lizard species found (see results) were *Podarcis muralis*, *P. hispanica*, *Psammodromus algirus* and *Lacerta lepida*. The common wall lizard, *P. muralis*, is a small lacertid lizard (60–76 mm adult snout-to-vent length, SVL) widespread in central Europe, although in the Iberian Peninsula it is restricted to mountainous areas of the northern half, where it occupies soil dwellings, talus and walls in shaded zones in forests (Martin-Vallejo et al. 1995; Salvador 1998). The Iberian wall lizard, *P. hispanica*, is a small (50–70 mm adult SVL) lacertid lizard of all over the Iberian Peninsula, common in rocky

habitats or artificial walls (Martin-Vallejo et al. 1995; Salvador 1998). The large psammodromus, *P. algirus*, is a medium-sized lizard (70–80 mm adult SVL) inhabiting both the perennial and deciduous Mediterranean forests of the Iberian Peninsula and northwest Africa (Carrascal et al. 1989; Díaz and Carrascal 1991; Martín and López 1998, 2002; Salvador 1998). The ocellated lizard, *L. lepida*, is a large lacertid lizard (140–245 mm adult SVL) widespread in Mediterranean habitats of the Iberian Peninsula, southern France and northwest Italy, from the sea level to Mediterranean high mountains (Castilla and Bauwens 1992; Salvador 1998).

Lizard censuses and vegetation sampling

Lizard censuses were conducted from April to July 2002, coinciding with the mating season of lizards, when they were particularly active. We marked 81 line transects 200 m in length distributed more or less evenly throughout the study area, at least 1–2 km apart, and chosen to cover homogeneous patches of forests of both types through all the altitudinal gradient (between 1200 and 1600 m). Transect census were made on days with favourable weather conditions (warm sunny days) and between 09:00 and 13:00 GMT, when lizards were more active. We identified and counted lizards flushed or observed in each transect and in a 10 m-wide belt, 5 m on each side of the survey line. This method provided relative abundance of lizards for each transect (Martín and López 2002). We also conducted additional surveys at similar hours and under similar weather conditions by walking haphazardly through all the area, lifting up stones and logs in order to confirm the presence of secretive semifossorial skinks and fossorial amphisbaenians in each type of forest. Survey effort for transects and additional surveys was similar in oak forests and pine plantations.

When we detected a lizard on a transect, we marked the point and, when the census had been completed, we took four 1 m transects, one at each of the four cardinal orientations radiating from the point where each individual was first sighted. We used a scored stick standing vertically at nine sample points (two points at 50 and 100 cm in each of the four transects, and the central point), and recorded the type of substrate at each point (grass, leaf litter, bare soil, or rocks). We noted whether there was tree cover above the sample point, the type of tree (oak or pine), and the subarboreal vegetation at each point. We classified this subarboreal vegetation in two types according to height and characteristics: herbaceous perennials (< 50 cm height; including species such as *Paeonia broteroi* or *Pteridium aquilinum*), and woody shrub species (< 50 cm height; including *Juniperus communis*, *Genista florida*, *Crataegus monogyna*, *Cytisus scoparius*, *Rosa pouzini*, *Rubus ulmifolius*, and *Lonicera periclymenum*). We noted the type of vegetation (herbaceous vs. shrub) and the height from the ground to the first contact of leaves with the stick. This variable provided an indication of the potential utility of this subarboreal vegetation as a refuge by

lizards (Martín and López 1998). Thus, a low height indicated that vegetation was close to the ground and provided a narrow refuge. Previous studies have shown the importance of plant cover at the ground level for lizards (Carrascal et al. 1989; Martín and López 1998). Also, for these lizard species, the subarboreal vegetation total height was not considered important because lizards move on the ground and below vegetation.

We calculated percent cover values for each habitat variable in the area surrounding each lizard (i.e., % contacts with each substratum and vegetation type, and height of potential refuges; for a similar sampling methodology see Martín and López 1998, 2002). We also noted the distances of each point where the lizard was observed to the nearest potential refuge (shrub or rock) and to the nearest sunny spot where lizards could bask (distance to open). Given the large size of the area surveyed and the high lizard density, and because we sampled each transect only once, the probability of repeated sampling of the same individual was very low. We therefore treated all measurements as independent.

To estimate the availability of microhabitats along each transect, we recorded the same variables as above at three points per transect (at 70, 140 and 200 m along the progression line). As we selected transects with homogeneous vegetation, we considered that three points were enough to describe the availability of microhabitats along each transect.

Data analysis

We compared the presence of any lizard species in relation to the type of forest (pine plantations vs. oak forests) by using Generalized Non-Linear Models (GLZM), with the dependent variable following a binomial distribution (i.e., presence or absence of any lizard species in each transect). We used Chi-squared tests to compare the presence of each species observed in each transect in relation to the type of forest.

We used principal component analysis (PCA) to reduce all the habitat variables to a smaller number of independent components. We performed a PCA on the points describing available microhabitats in both types of forests and in the lizard-observed microhabitat points. Original data (number of contacts) were normalised by means of square root transformation. The initial factorial solutions were rotated by the Varimax procedure (Nie et al. 1975). Thereafter, we used General Linear Models (GLM) to compare PC scores describing microhabitat characteristics of the two types of forests (pine vs. oak forest), and those used by each lizard species. Thus, we determined whether lizards used available microhabitats in a non-random fashion (for a similar procedure see Martín and López 1998, 2002).

We calculated an average value for microhabitat characteristics for each transect by obtaining the mean value of PC scores of the three points of each transect. These average PC scores reflected the available microhabitat

characteristics of each transect. We used these average PC scores to obtain a predictive model for the relative number of lizards observed in a transect (Maurer 1986; Verner et al. 1986; Rubio and Carrascal 1994; Martín and López 2002). Thus, we examined the relationships between PC scores (independent variables) and the relative abundance of lizards in each transect (number of lizards of all species censused in a transect, dependent variable) using forward stepwise General Regression Models (GRM). We also made separate similar comparisons between PC scores and the number of lizards of each species (i.e., relative abundance) observed in a transect.

Results

Lizard species and distribution

The comparison of the presence or absence of lizards in transects showed that oak forests and pine plantations did not significantly differ in the number of transects that presented at least some lizard species (GLZM, Wald $\chi^2=0.22$, $df=1$, $P=0.64$). However, the lizard species found in each type of forest were different (Table 1). Large psammodromus (*P. algirus*) only appeared in oak forests (Chi-squared test, $\chi^2_1=11.57$, $P=0.0007$). Also occluded lizards (*L. lepida*) were found only in oak forests, although their low appearance in transects might explain that differences did not reach significance ($\chi^2_1=0.51$, $P=0.48$). In contrast, common wall lizards (*P. muralis*) appeared only in pine plantations ($\chi^2_1=12.96$, $P=0.0003$). Iberian wall lizards (*P. hispanica*) seem to be more ubiquitous and appeared in both types of forests, and, although they tended to appear more often in transects within pine plantations than in oak forests, differences only approached significance ($\chi^2_1=3.29$, $P=0.07$).

In relation to other lizard species not censused in transects, we observed a few Schreiber's green lizards (*Lacerta schreberi*) in both oak and pine forests, but they were mainly near to riverine vegetation habitats. Also, in the

Table 1. Number of transects (%) in which a given lizard species was found, and average (\pm SE) number of individuals of each species found in 200 m transects performed in pine plantations ($n=27$) and oak forests ($n=54$).

| Lizard species | Presence in transects (%) | | Number of individuals (mean \pm SE) | |
|-----------------------------|---------------------------|------|---------------------------------------|-----------------|
| | Pine | Oak | Pine | Oak |
| <i>Podarcis muralis</i> | 22.2 | 0 | 0.81 ± 0.19 | 0 |
| <i>Podarcis hispanica</i> | 11.1 | 1.8 | 0.37 ± 0.12 | 0.02 ± 0.09 |
| <i>Psammodromus algirus</i> | 0 | 33.3 | 0 | 0.96 ± 0.22 |
| <i>Lacerta lepida</i> | 0 | 1.8 | 0 | 0.02 ± 0.02 |
| Any lizard | 40.7 | 46.3 | 1.26 ± 0.32 | 1.15 ± 0.23 |

additional surveys in oak forests we found other species: one skink (*Chalcides bedriagai*), and an amphisbaenian (*Blanus cinereus*), which have fossorial or semifossorial habits and were not represented in transects. No other lizard species was found in pine plantations even during additional surveys.

Microhabitat selection by lizards

The PCA for microhabitats available and those used by lizards produced four components that together accounted for the 73.1% of the variance (Table 2). The first PC (PC-1) was negatively correlated with the cover of rocky outcrops, and positively correlated with substrates with grass and leaf litter, with cover of trees at the canopy level, and with distance to the nearest refuge. The second PC (PC-2) was negatively correlated with the cover of shrubs and distance to the nearest open area. The third PC (PC-3) was negatively correlated with cover and minimum height from the ground of perennial herbaceous vegetation. The fourth PC (PC-4) was positively correlated with bare soil cover.

Overall, microhabitats available in oak forests and pine plantations were different to those used by lizards (GLM, model, Wilks $\chi^2 = 0.31$, $F_{4,16} = 32.56$, $P < 0.0001$; Figure 1). Differences were significant in relation to PC-1 ($R^2 = 0.62$, $F_{4,371} = 149.18$, $P < 0.0001$), PC-2 ($R^2 = 0.07$, $F_{4,371} = 6.78$, $P < 0.0001$) and PC-4 ($R^2 = 0.08$, $F_{4,371} = 8.46$, $P < 0.0001$), but not in relation to PC-3 ($R^2 = 0.02$, $F_{4,371} = 1.88$, $P = 0.11$). Oak forests and pine plantations differed only in the cover of bare soil (PC-4), which was significantly and relatively higher in pine plantations (Tukey's test, $P < 0.0001$), but not in other characteristics (PC-1 to PC-3, $P > 0.50$ in both cases).

Table 2. Principal components analysis for available and lizard microhabitat data.

| | PC-1 | PC-2 | PC-3 | PC-4 |
|---------------------------|--------------|--------------|--------------|-------------|
| <i>Substrate</i> | | | | |
| Rocks | -0.87 | 0.16 | 0.01 | -0.07 |
| Bare soil | -0.03 | -0.01 | 0.01 | 0.90 |
| Grass | 0.78 | 0.19 | 0.18 | -0.16 |
| Litter | 0.74 | -0.26 | -0.18 | -0.10 |
| <i>Vegetation</i> | | | | |
| Shrub cover | 0.05 | -0.91 | 0.07 | -0.04 |
| Shrub minimum height | 0.12 | -0.22 | -0.01 | -0.21 |
| Herbaceous cover | 0.13 | -0.01 | -0.68 | -0.23 |
| Herbaceous minimum height | -0.04 | 0.01 | -0.80 | 0.10 |
| Tree cover | 0.66 | 0.03 | -0.25 | 0.07 |
| Distance to refuge | 0.56 | 0.34 | 0.07 | 0.42 |
| Distance to open | 0.03 | -0.86 | -0.08 | 0.03 |
| Eigenvalue | 2.69 | 1.86 | 1.25 | 1.14 |
| % Variance | 24.43 | 16.94 | 11.38 | 10.36 |

Bold values indicate significant correlations at $P < 0.001$ with the principal component.

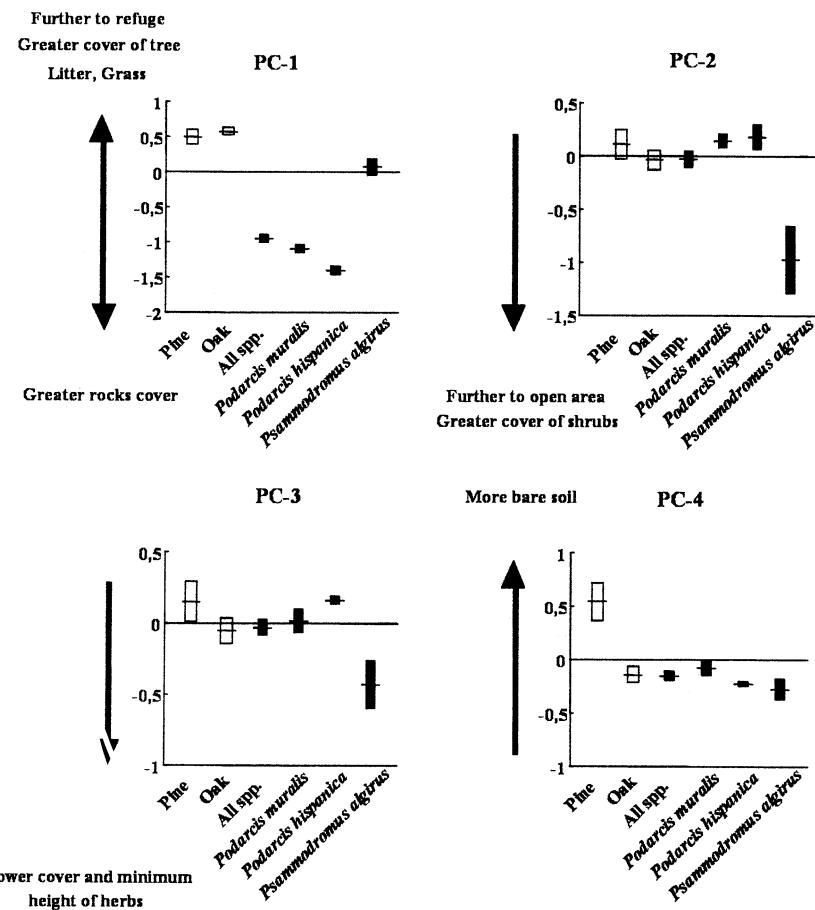


Figure 1. Mean (± 1 SE) of PC scores for microhabitat available in pine plantations and original oak forests (open boxes), and for microhabitat used by all lizard species, and by *Podarcis muralis*, *Podarcis hispanica* and *Psammodromus algirus* lizards (black boxes).

In relation to PC-1, in both forests (Tukey's test, $P=0.92$), available microhabitats had a relatively high cover of trees, and substrates with relatively high cover of grass and leaf litter far from refuges, but all lizard species selected areas with less trees and more rock substrates, and close to refuges (PC-1, $P < 0.0001$ in all cases). There were significant differences between microhabitats selected by *P. algirus* and the two wall lizards, *P. muralis* and *P. hispanica* (PC-1, $P < 0.0001$). However, the two wall lizards did not differ in microhabitat selected ($P=0.11$); both selected areas of relatively high rock cover (Figure 1).

Psammodromus algirus also selected microhabitats with a relatively high cover of shrubs and far from open areas (PC-2, Tukey's tests; $P < 0.0002$ in all cases), whereas cover of shrubs in microhabitats selected by both wall lizard

species did not differ from those available in both types of forest ($P > 0.70$ in all cases) (Figure 1). The cover and height of herbaceous vegetation (PC-3) was not correlated with habitat selection by any lizard species ($P > 0.09$ in all species). Finally, all lizard species selected microhabitats with relatively low cover of bare soil (PC-4), which was similar to available bare soil in oak forests (Tukey's test, $P > 0.91$ in both cases), but not in pine plantations, where substrates had a relatively higher proportion of bare soil ($P < 0.003$ in all cases) (Figure 1).

Lizard-habitat relationships

When analyzing the relative abundance of lizards of all species in each transect (number of lizards per transect; see Table 1) in relation to the average PC scores defining available microhabitat characteristic of each transect, we found a relationship between relative lizard density of all species and microhabitat characteristics (forward stepwise, GRM, model: $R^2=0.15$, $F_{1,79}=14.31$, $P=0.0003$). Thus, without considering the species, more lizards were found in transects when there were rocks rather than grass or leaf litter, when the distance to a refuge was relatively short, and when the cover of trees was relatively low (PC-1, $\beta=-0.39$). Other habitat variables (PC-2, PC-3 or PC-4) were not significantly related to overall lizard abundance ($P > 0.25$).

When analyzing the relative abundance of each lizard species separately, results showed that this relationship was similar for the number of individuals of *P. muralis* censused in each transect, which changed in relation to microhabitat characteristics defined by PC-1 ($\beta=-0.45$) but not to PC-2, PC-3 or PC-4 (GRM, $R^2=0.20$, $F_{1,79}=20.55$, $P < 0.0001$). However, in the case of *P. hispanica*, the number of individuals changed in relation to microhabitat characteristics defined by PC-1 ($\beta=-0.24$) and PC-4 ($\beta=0.26$) (GRM, $R^2=0.14$, $F_{2,78}=6.10$, $p=0.003$). Thus, *P. hispanica* lizards were more abundant in transect with rocky outcrops, relatively close to the nearest refuge, and low cover of trees, rather than in substrates of grass, leaf or bare soil. In contrast, the abundance of *P. algirus* did not seem to depend on microhabitat characteristics defined by PC scores.

Discussion

Microhabitat selection and lizard-habitat relationships

Our surveys showed striking differences in lizard species found in oak forests and in pine plantations. Lizard species found in natural oak forests were *Psammodromus algirus*, *Podarcis hispanica* and *Lacerta lepida*, although this later species is more abundant in lowland holm oak forests (Castilla and Bauwens 1992; L. Amo, unpublished data), and, only occupied marginal

habitats in deciduous oak forests. However, when pine plantations replaced the natural oak forest there is a loss of two typical species of oak forests (*P. algirus* and *L. lepida*). In contrast, pine plantations support only the two wall lizards, *P. hispanica* which also inhabits oak forests, and *P. muralis*. Natural pine forests, situated at higher altitude are also characterized by the presence of *P. muralis* and *P. hispanica* lizards, with the occasional presence of a few *Lacerta monticola cyreni* lizards, which typically inhabit rocky scree at higher altitude above the tree line (Salvador 1998). Therefore, the ancient conversion of oak forests to pine plantations seems to have altered the lizard community, with a loss of two typical species of oak forests (*P. algirus* and *L. lepida*) and a colonization of *P. muralis* lizards from higher altitude natural pine forests.

Lizards did not use habitat at random, and each lizard species has some specific microhabitat requirements to optimize their thermoregulatory, anti-predator and foraging requirements (e.g., Carrascal et al. 1989; Díaz and Carrascal 1991; Castilla and Bauwens 1992; Martín and López 1998, 2002). These specific differences in microhabitat requirements may explain the absence of some lizard species typical of oak forests in pine plantations. Pine and oak forests differed in the characteristics and structure of microhabitats, with pine plantations showing relatively higher cover of bare soil substrates than oak forests. This characteristic may affect fundamentally to *P. algirus* lizards that use low bushes and substrates with abundant leaf litter cover to hide from predators (Martín and López 1998). This species also selected microhabitats with a high cover of dense shrubs, far from open areas. In contrast, *Podarcis* lizards selected habitats with rocky outcrops and with a low cover of trees, where these lizards may encounter sunny places for basking and low distances to rock crevices in which these species typically seek refuge. Microhabitat with such characteristics can be found either in pine plantations or in oak forests, which may explain the presence of *P. hispanica* in both types of forests. In contrast, the presence of *P. muralis* in pine plantations but not in oak forests located at similar altitude suggests a link between the distribution of this species and pine forests. This is probably due to differences in microclimatic conditions between pine plantations and oak forests. Unfortunately, we have not microclimate data of both forests. However, according to the dependence of microclimate conditions of *P. muralis* (Guisan and Hofer 2003), our results suggest that pine plantations probably present particularly favourable microclimate conditions that might have favoured the colonization of lowland areas by *P. muralis*, a species usually found at higher altitude in natural pine forests closely related to the Euro-Siberian climatic region (Salvador 1998; Guisan and Hofer 2003). Therefore, pine plantations might have contributed to the expansion of the southern and altitudinal limits of *P. muralis* distribution in the Iberian Peninsula, in areas otherwise occupied by typical Mediterranean lizard species, such as *P. algirus*.

These explanations seem to be supported by the correlation between relative lizard abundance and microhabitat characteristics. Although each species appeared to have some specific habitat requirements, the general patterns of

abundance in relation to habitat structure were very similar between species. Thus, the number of individual lizards depended on the presence of rocky substrates, low cover of canopy of trees, and the availability of refuges. These results are similar to those from previous studies (Taylor and Fox 2001). However, when considering each species separately, we found differences in microhabitat selection. For example, relative higher abundance of *P. muralis* lizards was found in transects with rocky substrates, low cover of canopy of trees, and low distances to refuges, whereas relatively higher abundance of *P. hispanica* lizards was related to transects with similar microhabitats characteristics than those of *P. muralis* but also with low substrates of bare soil. In contrast, *P. algirus* relative abundances did not seem to be correlated to availability of microhabitat characteristics of transects, therefore, this species seems to be more linked to forest than *Podarcis* spp., which are associated to rocky areas and as a consequence, their populations present contagious distributions (Salvador 1998).

Implications for the forest management

From the perspective of conservation and management of lizards, pine plantations seem not to contribute so much to the diversity of lizards' species. Reforestation with pines seems to imply a loss of oak species such as *P. algirus* and *L. lepida*, but seems to favour the particular expansion of *P. muralis*. Wall lizards (*P. muralis* and *P. hispanica*) are associated to rocky areas inside pine forests. Therefore, populations of wall lizards may be protected just by conserving rocky areas inside pine plantations. This is important because the Guadarrama Mountains are the southernmost limit of the distribution of *P. muralis*.

In other areas of pine plantations, especially at lower altitude, a good method to increase lizard diversity may be to allow the recolonization by oaks in the understory of pine plantations. This is possible because in pine plantations in the original area occupied by oaks, pines are exclusively maintained by human activities. Without human management, oaks may gradually invade and recolonize the area. This would have an added benefit of reducing fire frequency because oak forests are less flammable than pine forests (Calvo et al. 2003). This may also help to eliminate traditional measures against fire inside pine plantations, such as clear cutting techniques that are often employed to create areas without trees and shrubs to prevent the fire expansion. These areas without any shrubby vegetation not only prejudice soil characteristics (Schmitz et al. 1998) but also decrease habitat quality for lizards (Ryan et al. 2002; this paper). Furthermore, removing of dead vegetation and clearing of underbrush to prevent fires often eliminate potential refuges available to lizards (James and M'Closkey 2003). Similar results were obtained when comparing beetles species in clear cuts and following stages of vegetation succession (Similä et al. 2002). Shrubs may provide refuge for lizards, as well as insects for feeding.

The elimination of some pines to create open areas without many trees but with shrubby vegetation may be a good tool to improve lizard diversity in pine plantations. Dense tree canopy do not allow sunlight to reach the ground. Thus, open areas, with scarce trees, may allow lizards to bask, which may enhance lizard populations. Other studies have reported an increase in lizard abundance within deforested areas (Enge and Marion 1986; Goldingay et al. 1996; Renken et al. 2004) or at forest edges (Schlaepfer and Gavin 2001), which may be explained by the abundance of basking places within these deforested areas (Renken et al. 2004). Thus, according to the “intermediate disturbance hypothesis”, these results suggested that disturbances can promote the coexistence of species (Grime 1974; Connell 1978; Pickett and White 1985; Huston 1994) and promote high diversity of lizards’ species. Moreover, worldwide patterns in lizard abundance show that hotter, drier areas support more lizard species and individuals than cooler forested areas (Pianka 1988).

Therefore, the maintenance of oak stands inside pine plantations, with all the shrubs associated to this type of forest, should favour the maintenance of diversity and abundance of lizard’s populations. This agrees with previous results that found reptiles to be more abundant in mixed forests than in clear-cuts and pine plantations (Ryan et al. 2002). Similar results indicated the impoverishment of birds’ species in pine plantations in relation to the native vegetation of a concrete area (Sekercioglu 2002). The clearing of some pines in some areas of plantations with the encouragement of deciduous trees such as oaks and undergrowth are also forest managements proposed to favour the bird’s abundance and richness (Potti 1985; Carrascal and Tellería 1990) as well as plant diversity (Izco 1984). Thus, maintaining and favouring habitat heterogeneity may help maintain a high diversity, not only of lizards but also of other taxa, by providing a large number of different niches (Fischer et al. 2004).

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Tracking the effects of one century of habitat loss and fragmentation on calcareous grassland butterfly communities

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Abstract Habitat loss and fragmentation are known to reduce patch sizes and increase their isolation, consequently leading to modifications in species richness and community structure. Calcareous grasslands are among the richest ecosystems in Europe for insect species. About 10% (1,150 ha) of the total area of a calcareous ridge region (Calestienne, Belgium) and its butterfly community was analysed over a timeframe of about 100 years. Since 1905 to present day (2005), the Calestienne region has undergone both calcareous grassland loss and fragmentation: not only did calcareous grassland size decrease and isolation increase, but also, the number of calcareous grassland patches within the landscape increased until 1965, and subsequently decreased, clearly reflecting the effects of fragmentation. These processes have had a profound effect on the butterfly community: extinction and rarefaction affected significantly more often specialist species, which means that generalist species are more and more overrepresented. This ecological drift, i.e. the replacement of specialists by generalists in species assemblages is likely to be a general effect of habitat loss and fragmentation on natural communities.

Keywords Ecological drift · Generalist species · Habitat loss · Habitat fragmentation · Land cover · Specialist species · Grassland · Butterflies · Community structure

Introduction

The current extinction of many species is strongly related to habitat fragmentation and loss (Andrén 1996; Fahrig 1997) resulting from the destruction and deterioration of natural and

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semi-natural habitats (Fahrig and Merriam 1984; Wilcox and Murphy 1985; Saunders et al. 1991; Harrison and Bruna 1999). Habitat fragmentation and loss are known to reduce patch size and increase patch isolation (Andrén 1994), consequently leading to modifications in species richness and community structure (Wilcox and Murphy 1985; Kruess and Tscharntke 1994, 2000; Steffan-Dewenter and Tscharntke 1999, 2000; Tscharntke et al. 2002a, b).

Change in land use practices is the main factor causing habitat loss and fragmentation and hence also the main factor modifying species communities (Foster and Boose 1992; Austrheim et al. 1999; Cousins and Eriksson 2001; Maes and Van Dyck 2001). Foster and Boose (1992) show continuous shifts in plant species abundance and assemblages on a New England forest since the 1770s, following deforestation, then farming and finally reforestation. Maes and Van Dyck (2001) link the strong decline in butterfly species numbers since 1834, in Flanders (northern Belgium), to more intensive agriculture practices and built-on areas.

In Western Europe, landscapes have experienced deep and continuous changes in land use over the last two centuries, which has led to a severe decrease of many natural and semi-natural ecosystems. However, the effect of these drastic changes on species and communities still remain poorly documented. Most calcareous grasslands in Western Europe are semi-natural habitats, created by human activity over the past centuries (e.g. Balmer and Erhardt 2000). They are the result of ancestral agropastoral techniques, mainly extensive. Calcareous grasslands are biodiversity hotspots because they are amongst the richest plant and insect communities in Europe (Wallis de Vries et al. 2002). Since the beginning of the 20th century, agropastoral practices have been progressively abandoned due to a lack of economical interest and land use intensification, consequently endangering calcareous grasslands and their species communities (Balmer and Erhardt 2000).

Butterflies were used as models in this study because (1) it has already been shown that the amount of modifications in butterfly community structure and composition is proportional to the degree of fragmentation (Thomas 1991; New 1997); (2) they react quickly to environmental changes (Erhardt and Thomas 1991; Bourn and Thomas 2002); and (3) they are considered to be umbrella species (sustaining habitat to conserve them will also conserve many other taxa) and indicators of habitat quality (New 1997). Moreover, specialist (monophagous) butterfly species are more affected by environmental changes than generalist species (Erhardt and Thomas 1991; New 1997; Steffan-Dewenter and Tscharntke 2002; Tscharntke et al. 2002a). Calcareous grasslands are known as the most plant species rich ecosystem of northern Europe (up to 80 plant species/m²) (Wallis DeVries et al. 2002). This high biodiversity is also reflected in high butterfly species diversity (e.g. Krauss et al. 2003).

In this paper, we examine the effects of habitat loss and fragmentation on butterfly community structure in calcareous grasslands situated in southern Belgium. We take advantage of the simultaneous availability of (1) one century of surveys of the butterfly community in calcareous grasslands and (2) maps which allow us to track the changes in the distribution of calcareous grasslands in the landscape. We will attempt to relate current diversity patterns and community structure with habitat area and isolation through changes in land use over time.

Materials and methods

Study landscape

The Calestienne region, and more specifically the Viroin valley, occupies about 11,000 ha in southern Belgium (see inset in Fig. 1). This landscape is a mosaic of forests,

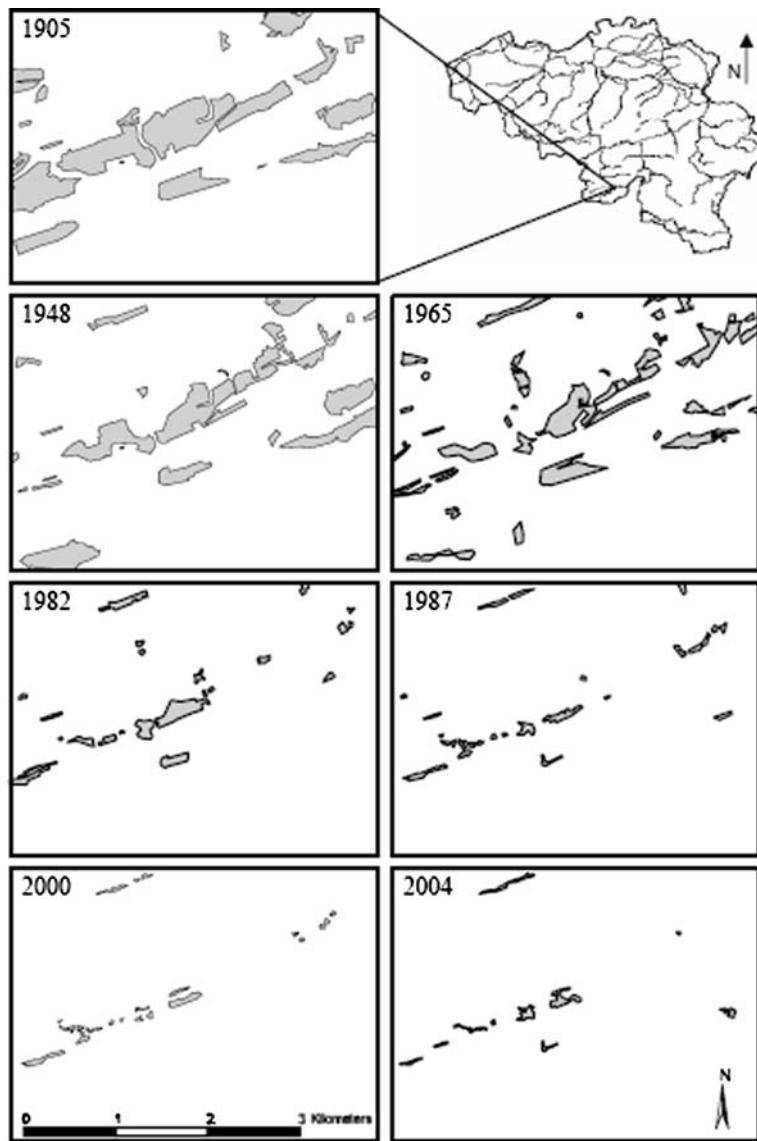


Fig. 1 Temporal development (1905–2004) of the calcareous grassland fragments in part of the Calestienne landscape

grasslands, thickets, farmlands and meadows. Calcareous hills are scattered throughout the landscape. Human settlement in this region dates back to at least 6,000 years, when the first farmers and herders arrived in the area, and has been sustained by a relatively dry local climate and the presence of fertile soils (Bruynseels and Vermander 1984). The proportion of calcareous grasslands in this landscape has recently declined as a result of rural migration and major transformations in agro-pastoral methods. It is worth noting that calcareous grasslands reach the north-western limit of their distribution range in the Calestienne region.

Approximately 1,150 ha, about 10% of total regional area, were analysed over a timeframe of about 100 years. The 1905 situation was based on an army map (scale 1/20,000); the 1948 map was based on a black and white aerial photograph, whereas the 1965, 1982, 1987 and 2000 landscapes were based on I.G.N. aerial photographs (Institut Géographique National). The current situation (2004) was based on field surveys (J. Butaye, personal communication). All the maps were imported in Arcview[®].

Landscape parameters

All xerophilous and mesophilous chalk grasslands were delineated for every year (1905, 1948, 1965, 1982, 1987, 2000, 2004) with Arcview[®] (Fig. 1). The area of every fragment was calculated using the same software. The distances from one fragment's centre to the centre of all the other fragments were measured using an Arcview[®] extension (Jenness 2003). These first two parameters then make it possible to calculate patch connectivity using Hanski's measurement (1999), which gives better results compared to all other connectivity measures such as distance to nearest patch or buffer measures (Moilanen and Nieminen 2002).

$$S_i = \sum_{j \neq i} \exp(-\alpha d_{ij}) A_j$$

where S_i is the connectivity of patch i , d_{ij} the centre-to-centre distance between patches i and j , and A_j area of patch j . Parameter α scales the shape of the negative-exponential function modelling the inverse cumulative proportion of individuals moving certain distances. This parameter shows strong interspecific variation, due to difference in species' mobility (e.g. Baguette et al. 2000) and intraspecific variation, due to landscape structure and population history (e.g. Mennechez et al. 2003). Indeed, the population parameter (α) varies widely between species in the studied landscape (e.g. for *Aporia crataegi*, $\alpha=1.9$; for *Melanargia galathea*, $\alpha=1.3$, Baguette et al. 2000). However, changes in α values did not modify the connectivity ranking (unpublished data); therefore, we decided to fix the value of α to 1.

The change in calcareous grassland number, area and connectivity over the six time lags were computed. Due to the lack of adequate data before the 1900s, the proportion of existing calcareous grasslands in 1905 is fixed as the maximum (100%).

Butterfly data

We examined butterfly species incidence (presence/absence) in the Calestienne region using a series of published surveys (Lambillon 1903; Lhomme 1923; Lameere 1940; Van Schepdael 1963; Fontaine et al. 1983; Goffart et al. 1992; Lafranchis 2000). Species listed during one time lag and not afterwards were regarded as extinct, which does not signify that they are or were not present elsewhere in Belgium. Those species that were mentioned in the Calestienne region were considered either as rare or as common according to the frequency at which they were observed by the respective authors. Three species (*Lamprides boeticus*, *Hipparchia fagi*, and *Pontia daplidice*) were excluded from the subsequent analyses because of their irregular migrant status. The composition of the butterfly communities of 1903, 1923, 1940, 1950, 1970, 1980, 1990 and 2000 was identified and was related to the landscape parameters listed above. Using this approach, we consider implicitly that all butterfly species recorded in the Calestienne region are present in our

study landscape, which is only a 10% subset of the whole region area. To evaluate the validity of this approach, 16 calcareous grasslands in part of this landscape were visited every two weeks during the butterfly's flight season of 2003, 2004 and 2005.

Specialist and generalist species

Because specialist species are more sensitive to environmental changes (Erhardt and Thomas 1991; New 1997; Tscharntke et al. 2002a, b) than generalist species, these two categories were treated independently. To distinguish between specialists and generalists, information from two different sources was used. First, Goffart and De Bast (2000) enabled us to identify species having a distribution limited to those Belgian regions characterized by the presence of calcareous grasslands. Secondly, species fidelity to calcareous grasslands, as a preferential or exclusive habitat, was based on Goffart et al. (1992). Only when a given species met both of these conditions, was it considered a habitat specialist. The dependence between the two criteria described above (generalist/specialist species vs. common/rare/extinct species) was analysed with a chi-squared test or a likelihood ratio test, when not enough data were available. The null hypothesis was that the frequency of a species in the community (common, rare or extinct) is independent of being a specialist or a generalist.

Relation between landscape parameters and butterfly communities

We used linear models to explore the relationships between a response variable (number of rare/common butterflies or number of extinct/rare/common specialist/generalist butterflies) and two possible predictor variables (average patch area and average patch connectivity, even if available landscape data did not coincide exactly with the butterfly surveys (1903–1905; 1948–1950; 1965–1970; 1982–1980; 1987–1990; 2000–2000). Response variables were tested against each predictor separately and both predictors together. The ‘Akaike’s Information Criterion’ was used to retain the best linear model (Akaike 1978).

Results

Whereas calcareous grasslands represented about 14.9% of the studied landscape in 1905, less than 0.7% still remains today (Table 1). Consequently, the average area of habitat patches has also continuously decreased, i.e. from 7.79 ha in 1905 to 0.82 ha in 2004. Table 1 and Fig. 2 show that the number of fragments in the Viroin Valley continuously

Table 1 Total patch area (ha), averages of all patch area (ha) and isolation (S_i), and patch number in the landscape for every studied years

| Time | Total patch area | Average patch area | Average patch connectivity | Patch number |
|------|------------------|--------------------|----------------------------|--------------|
| 1905 | 171.306 | 7.787 | 0.323 | 22 |
| 1948 | 126.240 | 5.050 | 0.291 | 25 |
| 1965 | 94.212 | 2.094 | 0.254 | 45 |
| 1982 | 27.554 | 1.060 | 0.086 | 26 |
| 1987 | 15.038 | 0.627 | 0.043 | 24 |
| 2000 | 9.350 | 0.425 | 0.031 | 22 |
| 2004 | 8.159 | 0.816 | 0.021 | 10 |

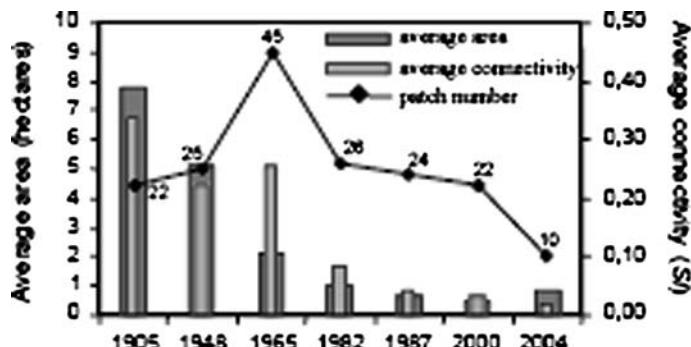


Fig. 2 Development of average habitat area, average connectivity and patch numbers over time

increased from 1905 until 1965. Subsequently, the number of fragments has decreased until present day. The average connectivity of a habitat patch, S_i , has continuously decreased from 0.323 at the beginning of the 20th century to only 0.021 at the beginning of the 21st century. Based on literature dating back to 1900s, 83 species of butterflies have been observed in the Calestienne (Appendix Table A1). It should be mentioned that some species, *Pyrgus armoricanus*, *Colias alfacariensis*, *Polyommatus thersites*, *Maculinea rebeli* and *Thymelicus sylvestris*, were only recorded as of 1923 or 1950. Each one of these species is easily confounded with one or several other species, very likely leading to misidentifications. Apart from these species, no new species were recorded during the studied time period.

Of these 83 species, only 32.5% are considered as not endangered (Red List of Walloon Region 1998). During the 2003, 2004 and 2005 field seasons, a total of 69 species were identified, 5 less than in 2000, all five are listed as vulnerable in the Red List of Walloon Region (1998). Four of these species (*Nymphalis antiopa*, *Hipparchia semele*, *Lycaena virgaurae*, and *Pyrgus serratulae*) have been getting rarer since the 1970s; only the first one still occurs in parts of the Calestienne region. The fifth, *Apatura ilia*, has been considered as a rare species since 1903, largely due to its ecology which makes it difficult to observe. Based on our criteria, almost 34.9% of the afore mentioned species (Appendix Table A1) are specialists of calcareous grasslands. Only one habitat specialist species (*Thecla betulae*) is not considered as endangered (Red List of Walloon Region 1998), although some authors (Lafranchis 2000) have reported its decline in Belgium. Extinction rates and the increase in rare species have continuously augmented since the 1900s (Table 2). The data in this study suggest that, since the beginning of the century, the proportion of both habitat specialists and generalists with a ‘common’ observed frequency decreased (Fig. 3), i.e. more species were ‘rare’ in 2004 than in 1903. Over this time period, *Arashnia levana* was the only species to increase its observed frequency from rare to common. Although no habitat generalists went extinct during this time period, nine specialist species did (Table 2). Over the entire 20th century, 64.8% habitat generalists and only 34.4% habitat specialists maintained their initially observed frequencies. For a given species, being a habitat specialist or habitat generalist significantly influenced its observed frequency (Table 3). Indeed, habitat specialists were more likely to be rare or extinct than are habitat generalists. This trend is all the more significant with the passing of time (Table 3).

Table 2 Specialist and generalist butterfly species number in relation to their observation frequencies (common, rare, extinct) over time

| Year | Specialist species | | | Generalist species | | |
|------|--------------------|------|---------|--------------------|------|---------|
| | Common | Rare | Extinct | Common | Rare | Extinct |
| 1903 | 18 | 7 | 0 | 48 | 5 | 0 |
| 1923 | 18 | 9 | 0 | 48 | 5 | 0 |
| 1940 | 15 | 12 | 0 | 48 | 5 | 0 |
| 1950 | 16 | 13 | 0 | 50 | 4 | 0 |
| 1970 | 11 | 12 | 6 | 38 | 16 | 0 |
| 1980 | 9 | 13 | 7 | 33 | 21 | 0 |
| 1990 | 8 | 14 | 7 | 32 | 22 | 0 |
| 2000 | 6 | 14 | 9 | 32 | 22 | 0 |

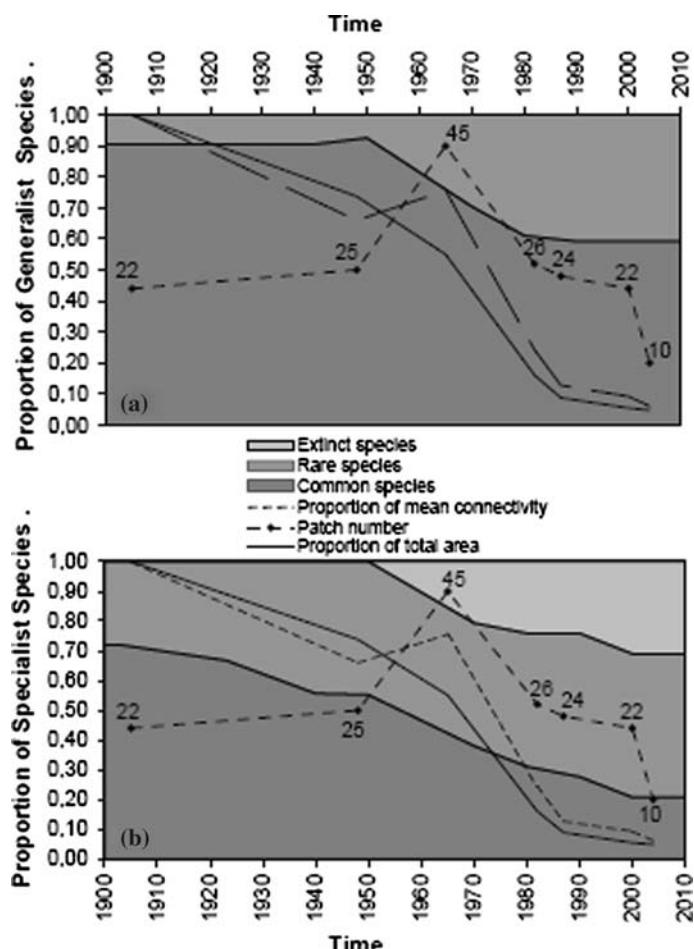


Fig. 3 Development of the generalist (a) and specialist (b) species communities since 1903. The proportions of common, rare, and extinct species are represented respectively in dark grey, average grey, and light grey. The proportion of total area of remaining calcareous habitat (continuous line), the proportion of mean connectivity (discontinuous line), and the number of remaining calcareous fragments (dotted line) are superposed on both figures (a) and (b)

Table 3 Chi-squared test or likelihood ratio value between species classified as habitat specialists/generalists and common/rare/extinct for each studied year

| Date | Chi-squared or likelihood ratio value | P |
|------|---------------------------------------|---------|
| 1903 | 4.206 | <0.05 |
| 1923 | 6.703 | <0.01 |
| 1940 | 13.102 | <0.001 |
| 1950 | 16.221 | <0.0001 |
| 1970 | 16.983 | <0.001 |
| 1980 | 18.536 | <0.0001 |
| 1990 | 19.268 | <0.0001 |
| 2000 | 23.136 | <0.0001 |

Common butterflies and common specialist/generalist species decreased linearly with decreasing average patch area and connectivity, whereas the number of rare butterflies and rare generalist species increased (Table 4). Rare and extinct specialist species were sensitive to average patch area; their numbers increased with decreasing area (Table 4).

Discussion

The change in landscape parameters measured in this study clearly shows that the calcareous grasslands of the Viroin Valley in the Calestienne region have been subject to the effects of habitat loss and fragmentation since at least 1905 (Table 1, Fig. 2). The alteration of the landscape, largely a consequence of changes in land use during the 20th century (Bruynseels and Vermander 1984), is clearly visualised by Figs. 1 and 2. The loss and fragmentation of calcareous grasslands have resulted in both a decrease in habitat area and connectivity and in fluctuations of habitat fragment number. The increase in habitat fragments until 1965 and subsequent decrease in fragment number since that time can be explained by a two-step process. At first, habitat loss induced fragmentation of large patches into several smaller, and consequently fragment number *increased*. Subsequently, as fragments *became* smaller and smaller, habitat loss *resulted* in the elimination of these fragments leading to a total decrease in number of fragments. This pattern has been

Table 4 List of the models by categories of species (extinct/rare/common and/or specialist/generalist)

| Regression coefficients | Analysis of Variance | | | Explanatory variable(s) used in the model | | |
|-------------------------|----------------------|--------|------|-------------------------------------------|----------------------|------------------------------|
| | R ² | F | dl | P | Average patch area ↓ | Average patch connectivity ↓ |
| Rare butterflies ↑ | 0.990 | 153.26 | 2, 3 | <0.001 | Yes | Yes |
| Common butterflies ↓ | 0.946 | 26.12 | 2, 3 | <0.02 | Yes | Yes |
| Common specialists ↓ | 0.973 | 53.38 | 2, 3 | <0.05 | Yes | Yes |
| Common generalists ↓ | 0.906 | 14.44 | 2, 3 | <0.03 | Yes | Yes |
| Rare generalists ↑ | 0.923 | 18.12 | 2, 3 | <0.03 | Yes | Yes |
| Rare specialists ↑ | 0.738 | 11.27 | 1, 4 | <0.03 | Yes | – |
| Extinct specialists ↑ | 0.895 | 34.18 | 1, 4 | <0.01 | Yes | – |

N.B.: The smallest values of AIC were selected to retain the best models. Analyses give five multiple regression models and two simple regression models for butterfly diversity in Calestienne. The tendency of each variable of species categories and of each explanatory variable is indicated by an upward pointing arrow if the variable tends to increase and by a downward pointing if it tends to decrease

predicted by a simulation model of landscape change (Andrén, 1994) and observed in other landscapes as well (e.g. Baguette et al. 2003). It is also important to note the slight increase in the average area of calcareous grasslands between 2000 and 2004. This can be explained by the vast calcareous grassland management and restoration campaign that has been active since the 1980s in the Calestienne region.

In Fig. 3, the percentage of calcareous grassland area, the number of habitat fragments and the butterfly species numbers are superposed. Two main conclusions can be drawn from these analyses. First of all, the increase in extinct and rare species within the butterfly community is particularly discernible as of the 1940s and 1950s. A similar increase in butterfly extinction numbers was observed in the Flanders (northern Belgium) by Maes and Van Dyck (2001) during the same time period (second half of the 20th century). At this time, more or less 73% of the original habitat surface still remains. According to Andrén (1994) and Fahrig (1997), fragmentation effects on species communities do indeed increase linearly until 20%–30% of original habitat in the landscape remains. However, beyond this threshold, a positive exponential relationship is observed between habitat fragmentation and its effects on species abundance and diversity. In addition to this threshold, Tilman et al. (1994) also highlight the existence of an extinction debt according to which a species is still present even though its habitat requirements are no longer met. In others words, some species will react immediately to the habitat changes whereas others will react with a certain delay. There may exist several reasons to explain why the threshold in our study appears much higher than that predicted by models ($\pm 70\%$ vs. 20%–30%). First of all, we assumed 100% habitat coverage in 1905, even though habitat loss most likely already occurred before this time period. However it is extremely hazardous to estimate calcareous grassland coverage before the 1900s because of the difficulty in identifying this habitat on older maps. Other explanations include the fact that threshold values vary between organisms and landscapes, amongst others (Andrén 1999).

The intensification of agriculture and afforestation of semi-natural habitat are mentioned as the principal causes of the changes observed in butterfly communities in Europe (Kudrna 1986; van Swaay 2002). Here, we show that the impoverishment of calcareous grassland butterfly communities corresponds to simultaneous and drastic changes in habitat availability and landscape structure, largely due to the abandonment of traditional agro-pastoral practices.

Secondly, regression analyses showed that all categories of species reacted to changes in landscape parameters. Surprisingly, rare specialist species were not affected by the decrease in connectivity; this may be due to the fact that local populations were already isolated and did not function as metapopulations. Finally, calcareous grassland specialists were more sensitive to changes in landscape parameters than generalists (specialist species went more often extinct or became rarer).

Therefore, due to habitat loss and fragmentation, ecological drift, a process similar to that of genetic drift where the least common alleles or organisms go extinct while the most common ones become more frequent, results in the impoverishment of natural communities. Indeed our results indicate that generalist species increasingly dominate the butterfly community. It is logical that habitat specialists, for which the calcareous grasslands are exclusive or preferential habitat, will be affected by habitat deterioration sooner and to a greater degree than habitat generalists (e.g. Steffan-Dewenter and Tscharntke 2002; Krauss et al. 2003). Indeed, generalist species can always use other habitats once calcareous grasslands have disappeared, whereas this is not the case for specialist species. However, the persistence of some specialist species depends on much more complicated processes

than the availability of suitable habitats. Indeed, previous studies have shown that specialist species such as *Lysandra bellargus* and *Maculinea arion* were maintained by grazing disturbance: these species occupy a very confined ecological niche and they have very strict requirements concerning the vegetation structure and—for *M. arion* at least—the presence of the ant host species (Thomas 1991). The above-mentioned species are extinct in the Calestienne region even though their host plants are still present. For other species such as *Maculinea rebeli*, for instance, extinction is likely to be related uniquely to the decline of its unique caterpillar host plant, *Gentiana cruciata* (Goffart et al. 1992). These examples illustrate the ‘species cascade’ or ‘ripple effect’ (Forman 1995) and iterate the importance of habitat quality in its globality, i.e. it is necessary to maintain both high quality abiotic and biotic conditions in focal habitats to enable species to survive. The previous examples also emphasise the need for considering conservation efforts at the landscape scale (Baguette and Mennechez 2004): even the largest calcareous grassland fragment in the study landscape (2.4 ha in 2004) does not host all the specialist species remaining today. The establishment of networks of calcareous grasslands should allow the remaining fragments to be connected by individual movements and accordingly should permit the long-term persistence of the remaining species in the landscape.

Finally, we would like to address a possible criticism about the generalization of historical regional surveys to document patterns and processes at the landscape scale. As mentioned before, we infer the presence in our study landscape of all butterfly species listed in the whole Calestienne region. Our field survey (2003, 2004 and 2005) provided evidence of the presence of 69 species, 5 less than in 2000 (Lafranchis 2000). Four species had suffered from regional extinction, whereas the status of *Apatura ilia*, a forest species flying occasionally in calcareous grasslands is unclear due to its lack of detectability. Given these results, our generalization procedure should be considered as acceptable.

Conclusion

The extinction and rarefaction phenomena observed for the specialist species are rather linked to the fragmentation and loss of calcareous grasslands, whereas for generalist species, these processes appear to be linked to important changes observed in the landscape structure as of the 1950s. Indeed, a decrease in habitat fragment number increases the isolation between habitats, rendering the habitat specialist persistence dependent on their dispersal capacities. This is less so for habitat generalists, which can occupy several different habitats and will consequently be less susceptible than specialists to habitat fragmentation and habitat loss. The effects of the calcareous grassland restoration and management campaign have yet to be detected. This has been observed elsewhere as well and has been coined as ‘restoration lag’ by Huxel and Hastings (1999). Some clues indicate, however, that these restoration efforts are not fruitless, like the return in the Calestienne region of the butterfly *Mellitaea cinxia* during the exceptional warm flight season in 2003, after more than 30 years of absence.

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Appendix

Table A1 List of habitat generalist and specialist butterflies present in 1905 in the Calestienne and their current observation frequency (O.F.) (C=common, R=rare, and E=extinct)

| Family | Species | O.F. |
|-----------------------|-----------------------------------------------------------|------|
| 54 generalist species | | |
| Nymphalidae | <i>Aglais urticae</i> (Linné, 1758) | C |
| | <i>Apatura ilia</i> (Denis and Schiffermüller, 1775) | R |
| | <i>Apatura iris</i> (Linné, 1758) | R |
| | <i>Aphantopus hyperantus</i> (Linné, 1758) | C |
| | <i>Araschnia levana</i> (Linné, 1758) | C |
| | <i>Argynnis paphia</i> (Linné, 1758) | C |
| | <i>Clossiana euphrosyne</i> (Linné, 1758) | R |
| | <i>Clossiana selene</i> (Denis and Schiffermüller, 1775) | R |
| | <i>Coenonympha pamphilus</i> (Linné, 1758) | C |
| | <i>Cynthia cardui</i> (Linné, 1758) | C |
| | <i>Erebia medusa</i> (Denis and Schiffermüller, 1775) | C |
| | <i>Euphydryas aurinia</i> (Rottemburg, 1775) | R |
| | <i>Fabriciana adippe</i> (Denis and Schiffermüller, 1775) | R |
| | <i>Hipparchia semele</i> (Linné, 1758) | R |
| | <i>Inachis io</i> (Linné, 1758) | C |
| | <i>Issoria lathonia</i> (Linné, 1758) | R |
| | <i>Lasiommata maera</i> (Linné, 1758) | R |
| | <i>Lasiommata megera</i> (Linné, 1767) | C |
| | <i>Limenitis camilla</i> (Linné, 1764) | C |
| | <i>Maniola jurtina</i> (Linné, 1758) | C |
| | <i>Melitaea cinxia</i> (Linné, 1758) | R |
| | <i>Mellicta athalia</i> (Rottemburg, 1775) | R |
| | <i>Nymphalis antiopa</i> (Linné, 1758) | R |
| | <i>Nymphalis polychloros</i> (Linné, 1758) | R |
| | <i>Pararge aegeria</i> (Linné, 1758) | C |
| | <i>Polygonia c-album</i> (Linné, 1758) | C |
| | <i>Pyronia tithonus</i> (Linné, 1771) | C |
| | <i>Vanessa atalanta</i> (Linné, 1758) | C |
| Hesperiidae | <i>Carcharodus alceae</i> (Esper, 1780) | R |
| | <i>Carterocephalus palaemon</i> (Pallas, 1771) | R |
| | <i>Hesperia comma</i> (Linné, 1758) | R |
| | <i>Ochlodes venatus</i> (Bremer and Grey, 1853) | C |
| | <i>Thymelicus lineola</i> (Ochsenheimer, 1808) | C |
| | <i>Thymelicus sylvestris</i> (Poda, 1761) | C |
| Lycaenidae | <i>Callophrys rubi</i> (Linné, 1758) | C |
| | <i>Celastrina argiolus</i> (Linné, 1758) | C |
| | <i>Cyaniris semiargus</i> (Rottemburg, 1775) | R |
| | <i>Lycaena phlaeas</i> (Linné, 1761) | C |
| | <i>Lycaena tityrus</i> (Poda, 1761) | R |
| | <i>Lycaena virgaureae</i> (Linné, 1758) | R |
| | <i>Neozephyrus quercus</i> (Linné, 1758) | C |
| | <i>Nordmannia ilicis</i> (Esper, 1779) | C |
| | <i>Plebejus argus</i> (Linné, 1758) | R |
| | <i>Polyommatus icarus</i> (Rottemburg, 1775) | C |
| | <i>Satyrium w-album</i> (Knoch, 1782) | R |
| Papilionidae | <i>Papilio machaon</i> (Linné, 1758) | C |

Table A1 continued

| Family | Species | O.F. |
|-----------------------|-------------------------------------------------------------|------|
| Pieridae | <i>Anthocharis cardamines</i> (Linné, 1758) | C |
| | <i>Aporia crataegi</i> (Linné, 1758) | R |
| | <i>Colias crocea</i> (Geoffroy, 1785) | C |
| | <i>Colias hyale</i> (Linné, 1758) | C |
| | <i>Gonepteryx rhamni</i> (Linné, 1758) | C |
| | <i>Pieris brassicae</i> (Linné, 1758) | C |
| | <i>Pieris napi</i> (Linné, 1758) | C |
| | <i>Pieris rapae</i> (Linné, 1758) | C |
| 29 specialist species | | |
| Nymphalidae | <i>Argynnis aglaja</i> (Linné, 1758) | R |
| | <i>Chazara briseis</i> (Linné, 1764) | E |
| | <i>Clossiana dia</i> (Linné, 1767) | R |
| | <i>Coenonympha arcania</i> (Linné, 1761) | C |
| | <i>Erebia aethiops</i> (Esper, 1777) | E |
| | <i>Fabriciana niobe</i> (Linné, 1758) | R |
| | <i>Melanargia galathea</i> (Linné, 1758) | C |
| Hesperiidae | <i>Erynnis tages</i> (Linné, 1758) | C |
| | <i>Pyrgus armonicanus</i> (Oberthür, 1910) | E |
| | <i>Pyrgus malvae</i> (Linné, 1758) | C |
| | <i>Pyrgus serratulae</i> (Rambur, 1839) | R |
| | <i>Spialia sertorius</i> (Hoffmannsegg, 1804) | R |
| | <i>Thymelicus acteon</i> (Rottemburg, 1775) | R |
| Lycaenidae | <i>Aricia agestis</i> (Denis and Schiffermüller, 1775) | C |
| | <i>Cupido minimus</i> (Fuesslin, 1775) | R |
| | <i>Glaucoopsyche alexis</i> (Poda, 1761) | E |
| | <i>Hamaeris lucina</i> (Linné, 1758) | R |
| | <i>Lysandra bellargus</i> (Rottemburg, 1775) | E |
| | <i>Lysandra coridon</i> (Poda, 1761) | R |
| | <i>Maculinea rebeli</i> (Hirschke, 1904) | E |
| | <i>Polyommatus dorylas</i> (Denis and Schiffermüller, 1775) | E |
| | <i>Polyommatus theristes</i> (Cantener, 1834) | E |
| | <i>Pseudophilotes baton</i> (Bergsträsser, 1779) | E |
| | <i>Satyrium pruni</i> (Linné, 1758) | R |
| | <i>Satyrium spini</i> (Denis and Schiffermüller, 1775) | R |
| | <i>Thecla betulae</i> (Linné, 1758) | R |
| Papilionidae | <i>Iphiclides podalirius</i> (Linné, 1758) | R |
| Pieridae | <i>Colias alfacariensis</i> (Ribb, 1905) | R |
| | <i>Leptidea sinapis</i> (Linné, 1758) | C |

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The distribution pattern of centipedes in four primeval forests of central Slovakia

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Abstract We investigated the distribution pattern of centipedes (Chilopoda) in four primeval forests of the western Carpathians, central Slovakia. The forests are located in two different mountain ranges (Kremnické vrchy and Pol'ana Mountains), which are exposed on either the southern (Boky, Rohy) or northern slopes (Pol'ana, Badín). In these forests, the influence of coarse woody debris (CWD) on centipede distribution was studied, by distinguishing sampling sites on the forest floor, close to CWD (c-CWD) and distant from CWD (d-CWD). In total, we collected 2,706 individuals from 20 species of centipedes. Average species richness and number of individuals per forest ranged from 8 to 12 species/m² and from 244 to 486 individuals/m². The oak forests on south facing slopes harboured several species, which did not occur in the more northern exposed fir-beech forests. Number of species as well as individuals, however, varied more within than between individual forests. Increase of species number and density was mainly caused by CWD and was more pronounced on the southern slopes ($P<0.001$), characterized by high temperatures and low precipitation, than on the northern slopes (n.s. to $P<0.01$), characterized by low temperatures and high precipitation. It was found that CWD did not generally increase (species) diversity.

Keywords Centipedes (Chilopoda) · Climate · Coarse woody debris (CWD) · Diversity · Primeval forest

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Introduction

Centipedes are widely distributed throughout the temperate regions of the world. Members of Lithobiomorpha and Scolopendromorpha are often encountered in loose leaf litter on the forest floor, in crevices under rocks and under the bark of decaying fallen trees, while representatives of Geophilomorpha mainly inhabit the upper soil layer. Some of the latter are essentially subterranean and capable of burrowing through the soil (Wallwork 1976). Species of all groups are generally considered to be carnivorous, although they may occasionally feed on decaying plant material (Lewis 1981). Centipedes do not possess a well-developed epicuticular wax layer, exhibit high cuticular transpiration rates (Mead-Briggs 1956) and they lack an efficient spiracular closing mechanism (Curry 1974). Hence centipedes are confined to microhabitats in which desiccation is greatly reduced, but flooding is avoided. (Tajovský 1999). Coarse woody debris (CWD) may constitute such microhabitats.

In primeval forests, CWD is a common and important structural element on the forest floor that provides food and shelter for many rare and threatened species, including vertebrates as well as invertebrates (Whiles and Grubaugh 1996; Ohlson et al. 1997). During the last few decades, several primeval forests of Slovakia containing considerable amounts of CWD have been designated as forest reserves. The forest reserves have the advantage of both protecting the full range of biodiversity and providing important references against which ecological situations in managed forests can be compared (Norton 1999).

For this study, we selected four primeval forests designated as either forest reserves (three cases) or as protected forests (one case) all containing high amounts of CWD. The main objective was to illustrate the influence of CWD on the distribution pattern of centipedes. Our hypothesis is: sites close to CWD will harbour higher species richness, higher density and also higher diversity than sites distant from CWD.

Material and methods

The study areas are situated in the western Carpathians, central Slovakia, in two distinct mountain ranges: the Pol'ana and Kremnické vrchy Mountains. Both mountain ranges are of volcanic origin and are covered by broad-leaved, coniferous or mixed forests, of which only fragments can presently be considered to be natural. Four study areas were chosen in primeval (natural) forests: either strictly protected forest reserves (Rohy in the Pol'ana mountains, and Boky and Badín in the Kremnické vrchy mountains) or classified as “protective forests on steep slopes” that have not been managed and are well preserved (Pol'ana—Pol'ana mountain range). The distances between the primeval forests range from 10 to 30 km. For more characteristics of the study areas see Table 1.

In each forest, 64 litter samples of 300 cm² were collected, including all O-horizons. We sampled sites close to (c-CWD: mean distance <10 cm, n = 32) and sites distant from (d-CWD: mean distance >200 cm, n=32). The minimum size of CWD chosen for sampling was represented by logs 20 cm in diameter and 200 cm in length. Minimum distances between sampling sites was 20 m. The total area coverage per forest and per c-CWD or d-CWD sites was 0.96 m². All forests were sampled in May and in July 2003, with specific logs chosen once only. All logs taken into consideration were at least moderately decayed (decomposition stage Z°2 according to Albrecht 1991).

Table 1 Main characteristics of the four primeval forests studied (Boky, Rohy, Pol'ana, Badín)

| | BoKy | Rohy | Pol'ana | Badín |
|--------------------------|--------------------------------------------------|--------------------------|--------------------------------------------|------------------|
| Mountain range | Kremnické vrchy | | | |
| Size of reserve [ha] | 176 | Pol'ana | Pol'ana | Kremnické vrchy |
| Aspect of slope | S, SW | 25 | 40 | 31 |
| Gradient of slope [°] | 10–40 | S, SW | E | N, NE |
| Altitude [m above s.l.] | 280–590 | 10–40 | 20–60 | 10–40 |
| Dominant tree species | <i>Quercus polycarpa</i> , <i>Quercus cerris</i> | 400–600 | 980–1100 | >2.0 |
| Crown closure | 0.8–2.0 | <i>Quercus polycarpa</i> | <i>Fagus sylvatica</i> , <i>Abies alba</i> | 2.0–2.0 |
| CWD [m ³ /ha] | 20–40 | 0.8–2.0 | 150–280 | 250–350 |
| Main soil type | eutric cambisol | 150–280 | dystric cambisol | dystric cambisol |
| Temperature in July (°C) | 18.5–20.0 | eutric cambisol | 12.0–16.0 | 12.0–16.0 |
| Annual rainfall (mm) | 600–700 | 18.5–20.0 | 800–1100 | 800–1100 |
| Nature reserve since | 1986 | 600–700 | 1981 | 1913 |

Climatic data from Lapin et al. 2002

Soil arthropods were extracted from the litter using modified Tullgren funnels. Determination of Lithobiomorpha and Scolopendromorpha was carried out using the identification keys in Loksa (1954) and Eason (1964, 1982). Several morphological features of Lithobiomorpha, which allow determination to the species level (e.g. female gonopods, modification of male legs), are only well-developed in the adult stage. The determination of Geophilomorpha was performed according to Rosenberg (1989).

Data analysis

Both time periods were pooled to achieve yearly sums. Thus, the number of data sets per forest was $n=32$, with 16 sampling sites at “c-CWD” and 16 sites at “d-CWD”. Most of the data was not normally distributed. Consequently, median \pm median absolute deviation (MAD) are given and Mann–Whitney U -test was performed to compare data sets between forests and between c-CWD and d-CWD sites within forests.

Species-area curves (species richness) and rarefaction diversity were calculated for each forest using the pooled data sets of scattered plots of 300 cm^2 ($n=32$) separately for c-CWD and d-CWD sites. Rarefaction is a procedure for analysing the number of species among collections, when all collections are scaled down to the same number of individuals. Our rarefaction analysis was fitted to regression lines ($y = a \ln(n) + b$). When the sample size is small, rarefaction diversity provides an alternative to conventional indices of species diversity such as Shannon diversity (H') (Smith and Grassle 1977; Hsieh and Li 1998).

Results

We collected 2706 individuals of centipedes belonging to the three orders Lithobiomorpha, Geophilomorpha and Scolopendromorpha. The Lithobiomorpha were most common (2213 ind.) and were represented by 13 species of the genus *Lithobius*. We found 669 adult individuals, which were determined to species level. Juveniles and post-juveniles appeared in a number of 1544 individuals. The Geophilomorpha (417 ind.) comprised six species belonging to five genera, whereas the Scolopendromorpha (76 ind.) were represented by a single species, *Cryptops hortensis* (Table 2).

Average centipede densities per forest were 244 ind./m^2 in Badín and 256 ind./m^2 in Boky (Kremnické vrchy mountain range), 368 ind./m^2 in Rohy and 486 ind./m^2 in Pol'ana (Pol'ana mountain range). Densities in forests on the same mountain range did not differ significantly ($P > 0.05$). We found no significant differences ($P > 0.05$) between the south facing forests (Boky vs. Rohy). However, we detected significant differences in densities ($P < 0.05$) between the north facing forests (Badín vs. Pol'ana).

Overall more species were collected at c-CWD than at d-CWD sites (Table 2). Eight of the 20 species found (*L. aeruginosus*, *L. agilis*, *L. erythrocephalus*, *L. melanops*, *L. lapidicola*, *L. subtilis*, *L. tricuspidata*, *Sch. nemorensis*) occurred only at c-CWD sites. When testing species richness between c-CWD and d-CWD sites, we found significant differences in all forests (Fig. 2). Species-area curves also demonstrate increased species richness at c-CWD sites when compared to d-CWD sites (Fig. 1). Differences in species-area curves between c-CWD and d-CWD sites were most pronounced in Boky and Pol'ana.

In total, 72% of the individuals were collected close to CWD. Comparing absolute numbers, densities were lowest at d-CWD sites in the forests on southern slopes (75 and 88 ind./m^2 in Boky and Rohy, respectively) and highest at c-CWD sites in the forests of

Table 2 Density of centipedes (ind./m²) in different forests of four primeval forests of central Slovakia

| | Southern slopes | | | | Northern slopes | | | |
|-------------------------------------|-----------------|-------|-------|-------|-----------------|-------|-------|-------|
| | Boky | | Rohy | | Pol'ana | | Badín | |
| | c-CWD | d-CWD | c-CWD | d-CWD | c-CWD | d-CWD | c-CWD | d-CWD |
| <i>Lithobius aeruginosus</i> | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| <i>L. agilis</i> | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>L. austriacus</i> | 38 | 1 | 29 | 2 | 1 | 4 | 1 | 0 |
| <i>L. erythrocephalus</i> | 2 | 0 | 4 | 0 | 6 | 0 | 7 | 0 |
| <i>L. forficatus</i> | 29 | 3 | 14 | 1 | 7 | 4 | 0 | 3 |
| <i>L. lapidicola</i> | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 0 |
| <i>L. lucifugus</i> | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| <i>L. melanops</i> | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>L. mutabilis</i> | 49 | 11 | 67 | 10 | 88 | 56 | 47 | 33 |
| <i>L. muticus</i> | 1 | 0 | 9 | 1 | 0 | 0 | 0 | 0 |
| <i>L. piceus</i> | 1 | 2 | 0 | 0 | 4 | 0 | 1 | 0 |
| <i>L. subtilis</i> | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| <i>L. tricuspis</i> | 2 | 0 | 20 | 0 | 1 | 0 | 0 | 0 |
| <i>Clinopodes linearis</i> | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 |
| <i>Geophilus insculptus</i> | 2 | 2 | 0 | 1 | 3 | 13 | 8 | 1 |
| <i>Necrophleopagrus longicornis</i> | 18 | 4 | 14 | 2 | 43 | 16 | 12 | 4 |
| <i>Schendyla nemorensis</i> | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 |
| <i>Strigamia accuminata</i> | 31 | 6 | 50 | 6 | 55 | 35 | 41 | 11 |
| <i>St. crassipes</i> | 8 | 2 | 2 | 1 | 5 | 0 | 2 | 5 |
| <i>Cryptops hortensis</i> | 0 | 0 | 0 | 0 | 43 | 11 | 18 | 4 |
| Lithobiomorpha adult | 136 | 20 | 170 | 19 | 132 | 74 | 75 | 43 |
| Lithobiomorpha (post-) juvenil | 241 | 41 | 405 | 55 | 278 | 262 | 144 | 118 |
| Lithobiomorpha total | 377 | 61 | 575 | 74 | 410 | 336 | 219 | 161 |
| Geophilomorpha total | 60 | 14 | 72 | 14 | 106 | 66 | 64 | 21 |
| Chilopoda total | 256 | | 368 | | 486 | | 244 | |
| | 437 | 75 | 647 | 88 | 559 | 412 | 301 | 186 |

In each forest we distinguished between sites close to c-CWD and distant from d-CWD

Pol'ana (559 ind./m²) and Rohy (647 ind./m²) (Table 2). In three of the four forests studied we found significant differences in densities between c-CWD and d-CWD sites (Fig. 2). These differences, as well as differences in species richness, were more pronounced in the forests on southern slopes than in the northern forests.

Diversity, calculated by a rarefaction analysis, was not in parallel to the results obtained for species richness. In the two forests on southern slopes the number of species calculated for 75 individuals at d-CWD sites was higher than at c-CWD sites (Table 3).

Discussion

It has been generally accepted that increased biotope heterogeneity increases species number (Anderson 1978; Rosenzweig 1995). In forest ecosystems, CWD is a structural element, which increases heterogeneity on the forest floor. In the primeval forest of Badín, in which a standing crop of 1100 m³/ha was measured in the optimal stage of development (Korpel 1995), the amount of CWD although varying over space and time was consistently high at a level of more than 200 m³/ha in each year. Locally, in this primeval forest CWD reached an amount of 455 m³/ha (Saniga and Schütz 2001). In contrast, managed forests rarely include more than 3 m³/ha CWD with diameters >10 cm (Ammer 1991).

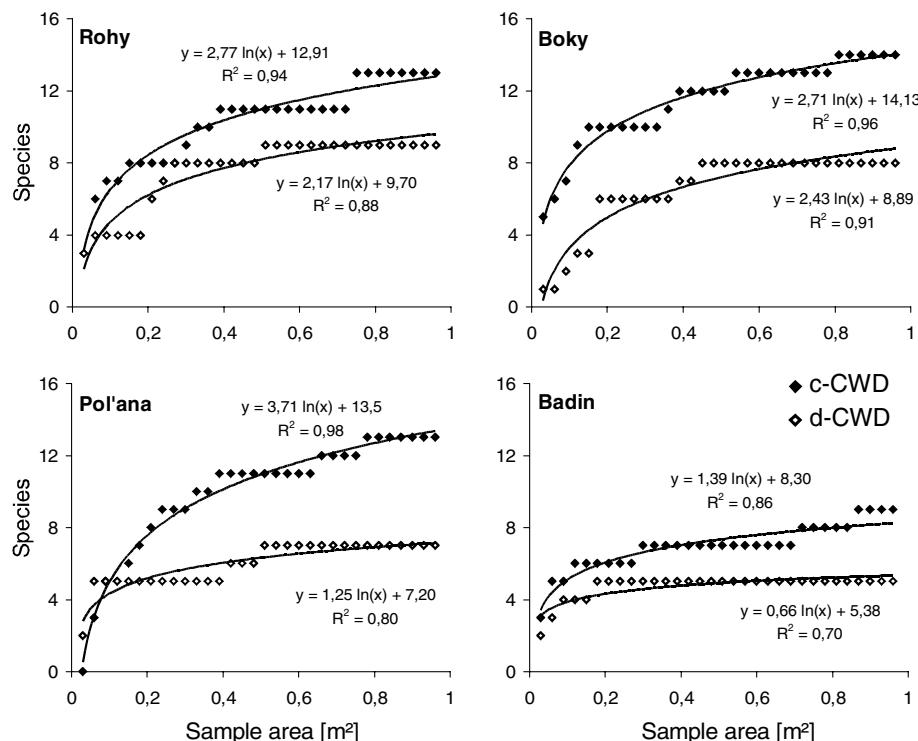


Fig. 1 Species-area curves for sites close to CWD (c-CWD) and distant from CWD (d-CWD) of the four primeval forests (Rohy, Boky, Pol'ana, Badín) of central Slovakia

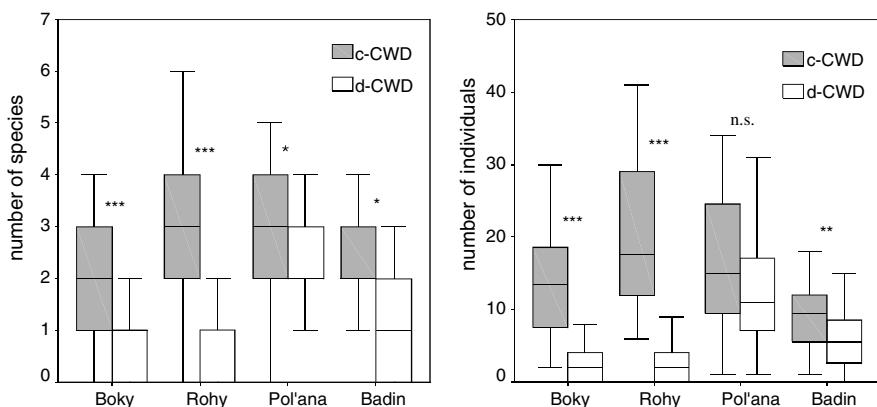


Fig. 2 Number of species and individuals of centipedes (Median, range, 25%- and 75%-percentile per 300 cm², $n=32$) in four primeval forests (Boky, Rohy, Pol'ana, Badín) of central Slovakia. Significant differences between sites close to CWD (c-CWD) and distant from CWD (d-CWD) are indicated: * $= P \leq 0.05$, ** $= P \leq 0.01$, *** $= P \leq 0.001$, n.s. = non significant

Effect of CWD

CWD not only improves the nutrient supply but also provides habitats for many species of different taxa (Harmon et al. 1986). Our results indicate that centipedes may benefit from CWD. Wind currents often accumulate a large amount of leaves near logs (Kappes et al. 2006), and therefore a dense litter cover creates habitats with stable microclimatic conditions (in respect of temperature and humidity) in the A-horizon and the lower humified organic layer (Oh-horizon), even when atmospheric conditions vary (Geiger et al. 1995).

Centipedes, like many other soil arthropods, are known to prefer such moist habitats and situations (Marra & Edmonds 1998). In an experimental study, Fründ (1987) was able to show that *L. mutabilis* and other Lithobiomorpha preferred humidity as high as 100%. The preference for moist conditions certainly results from the high transpiration rates as far as water vapour pressure deficiency occurs. Hadley (1994) showed that *Lithobius* spp. are most sensitive to desiccation.

Simultaneous effect of CWD and location

Centipedes are able to disperse and select for favourable locations when physical conditions become inappropriate. In Wytham Woods (England), centipedes migrated to CWD during warmer weather, but stayed in the litter layer during colder weather (Lloyd 1963). A higher water vapour pressure deficiency during warmer weather (Geiger et al. 1995) may have forced the centipedes to retreat from the sparse litter layer and seek for sites with dense litter layer close to CWD. Lloyd's observation is continued when comparing the relatively high number of individuals found close to CWD at the southern forests (characterized by a high insolation, low precipitation and high temperature) (Lapin et al. 2002) to the more northern forests (Lloyd 1963).

Six of thirteen *Lithobius* spp. only occurred in the forests on southern slopes. At least one of the species, *Lithobius melanops*, is known to be thermophilic (Spelda 1999). Also *Lithobius tricuspis* and *Lithobius austriacus*, the latter is one of the smallest lithobiomorphic species found during our investigations, also favoured damp and warm conditions near the logs on south facing slopes.

Centipedes, which are known for their high locomotory activity, may easily find appropriate sites for minimizing physiological stress. The sites close to CWD covered with a thick leaf litter layer and situated in the unpleasant surrounding of the southern slopes were obviously more attractive than the c-CWD sites of the northern slopes, situated in a more tolerable environment.

Table 3 Diversity according to rarefaction analyses for sites close to CWD (c-CWD) and distant from CWD (d-CWD) of four primeval forests situated in central Slovakia

| | # of species calculated for n=75 individuals | Result of regression | R ² |
|---------------|----------------------------------------------|----------------------|----------------|
| Boky c-CWD | 8.48 | 3.32 ln(n) - 5.85 | 0.96 |
| Boky d-CWD | 8.79 | 2.42 ln(n) - 1.66 | 0.90 |
| Rohy c-CWD | 7.95 | 2.10 ln(n) - 1.12 | 0.91 |
| Rohy d-CWD | 9.53 | 2.21 ln(n) - 0.01 | 0.85 |
| Pol'ana c-CWD | 7.34 | 2.46 ln(n) - 3.28 | 0.88 |
| Pol'ana d-CWD | 4.47 | 1.60 ln(n) - 2.44 | 0.82 |
| Badín c-CWD | 6.29 | 1.25 ln(n) + 0.89 | 0.70 |
| Badín d-CWD | 4.62 | 0.86 ln(n) + 0.91 | 0.83 |

All regressions were P<0.001

Comparison of managed and primeval forests

In deciduous forests of Central Europe, which were managed recently or in historical times, the species number is relatively low and ranges from 10 to 15 species (Poser 1988; Fründ 1991). In contrast, a faunistic survey of beech forests including primeval forests and forest reserves, exhibited a species number almost twice as high ($n = 27$, Stašiov 2001). Similarly, the primeval forests in this study supported more species than are the managed forests. However, we cannot rule out that additional topographic or regional factors may have influenced species number.

Centipedes in managed deciduous forests rarely exceed a density of 200 ind./m² (Loksa 1968; Ellenberg et al. 1986; Fründ 1987; Poser 1988; Jabin et al. 2004), whereas the primeval forests exhibited average densities of about 400 ind./m². We assume that the increased density is caused by the effect of CWD serving for stable climatic conditions when otherwise conditions on the forest floor become intolerable.

Conclusion

Primeval forests are characterized by a rich fauna of centipedes. Species richness and high density may mainly be caused by the presence of CWD. CWD assumingly creates a stable environment even when environmental conditions on the forest floor vary considerably and become intolerable. The beneficial effect of CWD was more pronounced in forests situated in a warm and dry climate than in forests situated in a cool and moist climate. The accumulation of CWD in managed forests should increase species number and abundance close to values known for primeval forests.

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***Tuber* spp. biodiversity in one of the southernmost European distribution areas**

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Abstract The aims of this paper were to study the genetic diversity within and among 6 *Tuber* taxa, the phylogenetic relationships and the spatial distribution of truffles from the Basilicata region (southern Italy). Molecular analyses, using the internal transcribed spacer region, microsatellites, minisatellites and random amplified polymorphic loci revealed the highest expected intra-specific heterozygosity ($He=0.30$) in *T. aestivum*, followed by that of *T. mesentericum* ($He=0.22$). *T. borchii* ($He=0.17$), *T. magnatum* ($He=0.16$), *T. aestivum* fo. *uncinatum* ($He=0.12$) and *T. brumale* fo. *moschatum* ($He=0.09$) showed a lower average heterozygosity. The whole set of markers were demonstrated to be useful in clearly differentiating *Tuber* taxa, separating them in two distinct groups and in five sub-clusters, each corresponding to one single taxon. The first cluster (*T. borchii*, *T. magnatum* and *T. brumale* fo. *moschatum*) was more differentiated than the second one (*T. aestivum*, *T. aestivum* fo. *uncinatum* and *T. mesentericum*). *T. brumale* fo. *moschatum* was the most differentiated *Tuber* taxon. It was more related to the white truffles (the closely related *T. borchii* and *T. magnatum*) than to the remaining related black truffles *T. aestivum* and *T. mesentericum*. The amount of *Tuber* species richness was higher over the western side of Basilicata, in cold *Lauretum* and in *Castanetum* phytoclimatic Pavari's zones. A spatial genetic structure was detected for *T. aestivum*, as shown by the significant correlation between geographic and genetic distances ($r_s=0.32$; $P<0.0001$). Integration of molecular and geographic diversity patterns can allow the selection of sites for *Tuber* and *Tuber*-related biodiversity conservation.

Keywords Basilicata region · Biodiversity · Ecogeographic distribution · Molecular markers · *Tuber* taxa

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Introduction

Tuber spp. are ascomycetes belonging to Pezizales, a large group of ectomycorrhizal fungi growing in symbiosis with roots of several vascular plant species (angiosperms and gymnosperms). The ascoma of these fungi is a hypogeous complex apothecium, commonly known as a truffle. The geographic distribution of known truffle species (about 100) mainly covers the temperate zones of the northern hemisphere, with at least three differentiation areas: Europe, South-East Asia and North America.

These ectomycorrhizal fungi are of great interest for the ecosystems they colonise because of the mutualistic associations and the advantages they provide to host plants (Pacioni and Comandini 1999).

A specific Italian Law regulates truffle collecting from natural stands to prevent the genetic erosion of the edible truffle species. The knowledge of both the spatial distribution and genetic diversity of the most relevant truffle taxa can provide a tool for planning in situ conservation programs. It is possible to identify a reserve by selecting the territory capturing the maximum of diversity within the least number of grid cells (Rebelo and Sigfried 1992). Nonetheless, the assessment of *Tuber* taxa spatial distribution is difficult given that the underground ascomata can be localised only using specifically trained dogs. Some truffle species (i.e., *T. aestivum* and *T. melanosporum*) produce a change in the rhizosphere of their host trees, the hydnosphere, visually perceived as a surface area characterised by a reduced growth or absence of grasses. This is due to allelopathic and chemical effects of some volatile organic compounds they produce (Pacioni and Comandini 1999). Strong ecological relationships exist between *Tuber* spp., host plants and soil type (Lulli et al. 1999). In Italy, truffles mostly grow at various altitudes (from a few metres above sea level to 800–1000 m), in calcareous soils with a sub-alkaline reaction ($\text{pH} \geq 7$ –8), while few taxa prefer acid and sub-acid soil (Pacioni and Comandini 1999). Soils must be permeable, well-aerated and well-drained, without stagnant water and also poor, in terms of N, P and Fe, but with a good content of Ca, K and S (Granetti 1994; Bencivenga 1998; Pacioni and Comandini 1999).

The geographical distribution patterns of truffles are not fully understood, although recently it has been shown that evolutionary lineages can be related to the biogeographical origin of the host species (Bertould et al. 1998, 2001; Martin et al. 2002; Moyersoen et al. 2003; Murat et al. 2004).

Within edible *Tuber* taxa, *T. aestivum* shows a genetic diversity higher than other black species such as *T. melanosporum* and *T. brumale* (Pacioni and Pomponi 1991; Gandeboeuf et al. 1997; Bertault et al. 1998, 2001; Mello et al. 2002; Murat et al. 2004; Weden et al. 2004), while among the white species, *T. magnatum* and *T. borchii* are characterised by a low intra-specific polymorphism (Longato and Bonfante 1997; Mello et al. 2002; Rubini et al. 2004).

Until recently, there have been no reports describing genetic diversity of southern Italian truffle species. Basilicata, a region in the South of Italy (Figs. 1, 3), has been lately discovered to be rich in *Tuber* species (Cerone et al. 1994, 1996, 2000, 2002a, 2002b; Tagliavini 1999; Marino 1999; Marino et al. 2003).

The region is diverse in topography: approximately 47% of it is represented by the Italian southern Apennines which characterise the north-western and southern regional sides; 45% is represented by eastern hills; 8% of the total area is level (valleys along rivers and the south-eastern Ionian coast) (ISTAT 1990). The western Apennine side is made up of mesozoic and tertiary calcareous rocks and of tertiary sedimentary rocks, while the

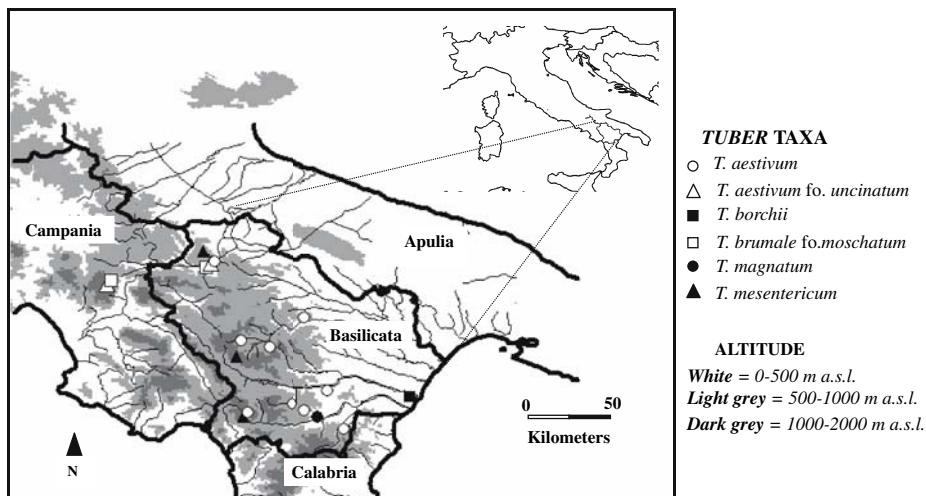


Fig. 1 Geographical distribution of 6 *Tuber* taxa analysed with four types of molecular markers

inland zones and the eastern hilly slopes are constituted by tertiary unconsolidated clayey marine and estuarine deposits. Finally, the Ionian coast strip is characterised by pleistocene marine, partly fluvial, sandy, clayey and loamy deposits (Regione Basilicata 2003).

The regional climate is on the average Mediterranean. A large climatic change can be observed across close areas at the same altitudinal level. The geographic distribution of vegetation zones is relevant to the localities of different truffle species host plants.

Four out of five different phytoclimatic areas (*Lauretum*, *Castanetum*, *Fagetum* and *Picetum*) can be identified in Basilicata according to Pavari's subdivision (Cantore et al. 1987). The *Lauretum* zone is composed of three sub-zones (warm, intermediate and cold), classified on the base of both rain and temperature levels. This zone is the widest (71% of the regional area) with a range extending from the Ionian coast to the pre-apenninic area (up to 800–900 m) and including the eastern hilly lands (500–600 m).

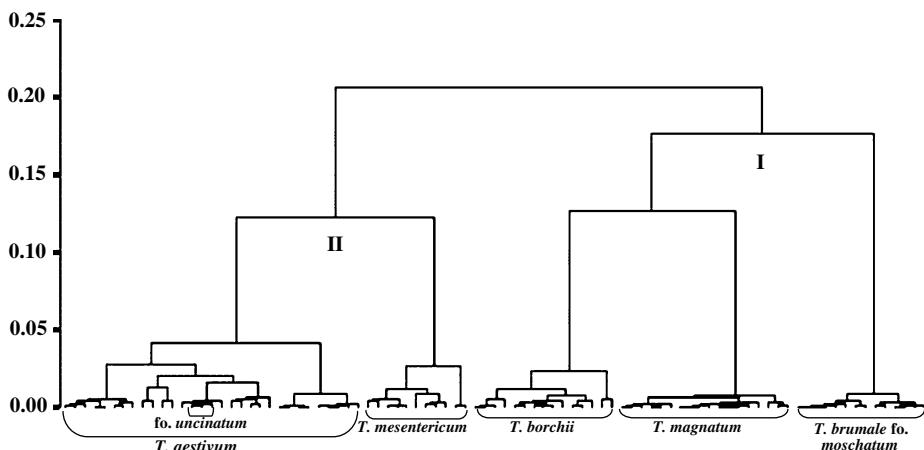


Fig. 2 Genetic relationships based on Dice's genetic distances and Ward's clustering method among 6 *Tuber* taxa from Basilicata region detected with four types of molecular markers.

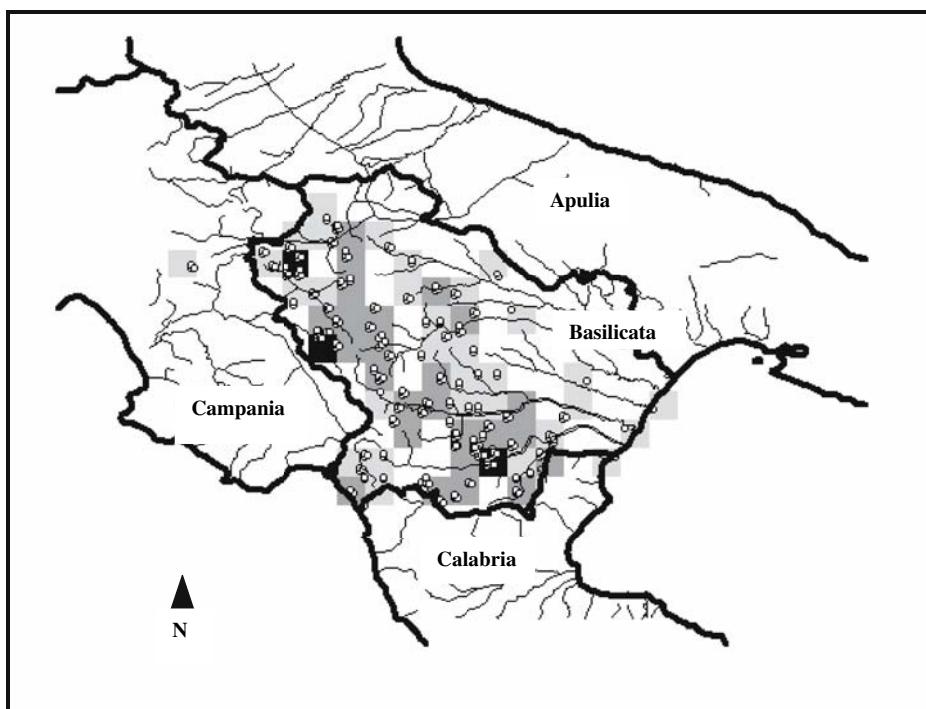


Fig. 3 Distribution area of edible *Tuber* taxa found in Basilicata (southern Italy) and species richness: 1–3 (light grey); 3–6 (dark grey); 6–9 (black); absence (white)

As reviewed by Granetti (1994), Mannozi Torini (1999) and Pacioni and Comandini (1999), within the *Lauretum* zone, the following truffle plant host genera are localised: *Quercus*, *Ostrya*, *Carpinus*, *Pinus*, *Cistus*, *Helianthemum*, *Corylus*, *Populus* and *Ulmus*. The *Castanetum* zone comprises 21% of the total surface and stretches along the Apennine ridge from 800–900 m to about 1200–1300 m a.s.l. The following truffle host trees are localised within this area: *Quercus* spp., *Castanea sativa* Mill., *Ostrya carpinifolia* Scop., *Carpinus betulus* L., *Salix* spp., *Corylus avellana*, *Populus* spp., *Fraxinus* spp., *Acer* spp. and *Tilia* spp.

There is a discontinuous strip of *Fagetum*, within the *Castanetum* zone and up to 1800–1900 m of altitude that comprises about 8% of the total area and is represented by the highest Apennine mountains (Volturino, Sirino and Pollino mounts) with a predominance of beech trees, turkey oak and hornbeam. Two spots belonging to the *Picetum* zone (Sirino and Pollino mount tops, higher than 1900 m) are also present.

The phytogeographic and pedological maps represent a tool which help to study truffle ecological distribution, while molecular markers can be useful to assess the extent of genetic diversity within and among taxa sampled in one of the southernmost European distribution areas.

The objectives of this study are to assess, through molecular markers, the genetic variation within and among different *Tuber* taxa naturally growing in the Basilicata region, evaluate genetic relationships among the edible regional *Tuber* taxa and summarise the spatial distribution patterns of *Tuber* species and forms in Basilicata.

Materials and methods

Morphological identification and molecular analyses

Identification of truffles was determined, according to Montecchi and Sarasini (2000) and Riocesset et al. (2001) scoring the following morphological and qualitative traits: ascoma shape and flavour, peridium and gleba size and structure, asci and ascospores shape and dimension.

Molecular analyses have been conducted only with DNA extracted from ascomata collected from December 2002 to October 2003. Eighty-nine ascomata belonging to 6 *Tuber* taxa (4 species and 2 forms) from 41 collecting sites were studied (Table 1 and Fig. 1).

DNA was extracted from ascomata, with peridium removed. An ascoma portion of about 1 cm³, pounded in 2.5–3 ml of extraction buffer (50 mM Tris–HCl pH 7.2; 50 mM EDTA pH 8.0; 3% w/v SDS) by using pestle and mortar, was mixed with one volume of chloroform/isoamyllic alcohol mixture (24:1) and then incubated in a water bath at 65°C for 15 min using Corex tubes (Falcon). After centrifugation at 5,000 rpm for 15 min at 4°C, supernatant with dissolved DNA was separated and the nucleic acids were precipitated with two volumes of –20°C ethanol (95%). Nucleic acids, once dried, were redissolved in 1× TE (Tris–EDTA) and visually scored through 0.8% agarose/TBE gel stained with ethidium bromide to determine DNA concentration.

The following four types of molecular markers were used: (a) internal transcribed spacer region with universal primers ITS1/ITS4 (White et al. 1990), (b) microsatellites [primer sequence: (GTG)₅] (Buscot et al. 1996), (c) minisatellites with primers formed by the internal repetitive sequences of the bacteriophage M13 (5'-GAGGGTGGCGGTTCT-3') (Latouche et al. 1997) and (d) randomly amplified loci (six decamer oligonucleotide primers) (RAPDs) (Table 2). For the RAPDs, primers UBPZ12, UBPZ20, UBPZ24, UBPZ23, which showed to be informative at inter-specific level (Figliuolo and Spagnoletti Zeuli 1993; De Gioia et al. 2005), and two new sequences UBPZ206 (5'-AAAGGACCCG-3') and UBPZ199 (5'-TGCCGAGCTG-3') were employed. Amplification reactions were performed using *iCycler* (BIORAD), containing Tris–HCl (20 mM, pH 8.4), KCl (50 mM), MgCl₂ (2.5 mM), dNTP mixture (0.25 mM), primer (0.2 μM), *Taq* DNA Polymerase (1 U) and genomic DNA. The PCR was programmed with an initial denaturation at 95°C for 3 min, followed by 45 cycles, each consisting of 1 min at 94°C, 1 min at 45°C and 1 min at 72°C, and a final elongation of 5 min at 72°C. A “touchdown” program for microsatellites amplification was used (Don et al. 1991). Amplified fragments were separated by electrophoresis on 2% agarose gel stained with ethidium bromide and visualised under UV light.

Table 1 Number of ascomata, collecting sites and ascomata per collecting site of 6 *Tuber* taxa from Basilicata (southern Italy) analysed with different types of molecular markers

| Species and forms | Ascomata No. | Collecting sites No. | Partition of (No. ascomata/collecting site) |
|--------------------------------------------|--------------|----------------------|------------------------------------------------|
| <i>Tuber aestivum</i> | 28 | 10 | (9)(6)(4)(2)(2)(1)(1)(1)(1) |
| <i>Tuber magnatum</i> | 18 | 18 | (1)×18 |
| <i>Tuber borchii</i> | 15 | 2 | (12)(3) |
| <i>Tuber brumale</i> fo. <i>moschatum</i> | 14 | 4 | (9)(2)(2)(1) |
| <i>Tuber mesentericum</i> | 11 | 4 | (4)(3)(3)(1) |
| <i>Tuber aestivum</i> fo. <i>uncinatum</i> | 3 | 3 | (1)×3 |
| All | 89 | 41 | Mean=2.17 |

Table 2 Molecular markers, PCR products and coancestry coefficient (θ) per marker detected within a sample of 89 *Tuber* ascocarpi from 6 different taxa

| Markers | PCR products | | $\theta=Fst$ |
|------------------------|----------------------|-----------------------|---------------|
| | No. fragments/primer | Base-pairs range (kb) | |
| ITS1/ITS4 | 5 | 0.5–1 | 0.57 |
| M13 | 6 | 0.6–1.1 | 0.43 |
| SSR (GTG) ₅ | 4 | 0.8–2 | 0.74 |
| UBPZ12 | 14 | 0.35–2.5 | 0.43 |
| UBPZ23 | 10 | 0.35–1.6 | 0.32 |
| UBPZ20 | 9 | 0.5–2 | 0.35 |
| UBPZ206 | 9 | 0.5–1.7 | 0.51 |
| UBPZ24 | 8 | 0.4–1.2 | 0.42 |
| UBPZ199 | 7 | 0.6–1.8 | 0.38 |
| Average 8.0 | | | Overall 0.45* |

*95% Confidence Interval using bootstrapping over loci: Upper=+0.51; Lower=+0.39

Statistical analyses

For each ascocarp, electrophoretic bands were recorded as present (1) or absent (0). Each band, at a given level of molecular weight, was interpreted as a single allele and each genotype as a single haplotype. The Dice's sharing banding index was used to estimate the genetic relationships among genotypes, adopting an algorithm implemented in SAS (Statistical Analysis System) (SAS 1993). The "Dice" genetic distance, which measures the number of unshared bands from multiple loci profiles for each genotypic pairwise comparison and for each type of genetic marker (Nei and Lee 1979), was calculated as:

$$GD_{ij} = 1 - \left[2N_{ij} / (N_i + N_j) \right]$$

where GD is the genetic distance between genotype i and j ; N_{ij} is the number of bands common to i and j (shared bands); N_i and N_j are the total number of bands for i and j , respectively. Therefore, a GD=0 indicates the identity between two individuals, while a GD=1 indicates complete diversity between them.

The genetic unbiased estimate of polymorphism was assessed using the expected heterozygosity (He) calculated as:

$$He = 1 - \sum_{i=1}^a p_i^2$$

where p_i is the frequency of allele i and a is the number of alleles (Weir 1996).

While the coancestry coefficient (θ), also defined as Wright's Fst statistics, which measures the ratio of sample allelic variance to total allelic variance, was used to evaluate the degree of differentiation among species (Weir 1996).

For a set of r population (species) with sample allele frequencies p_i ($i=1, 2, \dots, r$) and for allele A , this statistic can be defined as:

$$\theta = \left[\sum_i \frac{(\bar{p}_i - \bar{p})^2}{(r-1)} \right] / \bar{p}(1-\bar{p}) = s^2 / \bar{p}(1-\bar{p})$$

where \bar{p} is the average sample frequency of the allele over the samples and s^2 is the sample allelic variance (Weir 1996). The significance of θ was assessed by bootstrapping over loci (Lewis and Zaykin 2001). The inter-specific relationships were depicted by cluster analysis performed using the Ward's minimum-variance method that minimises variance within groups while maximises variance between them (SAS 1993). Only for the most widely distributed *T. aestivum* and its forma *uncinatum*, the nonparametric Spearman's rank-order correlation between geographical and genetic distance matrices was computed (PROC CORR) (SAS 1993). The geographic distance matrix (in metres) was obtained with DIVA-GIS software (Hijmans et al. 2002), while the genetic one was based on Dice's distances.

Ecogeographic distribution

The geographic distribution patterns of *Tuber* taxa, at a regional level, were described on the basis of the data published in the last decade (Cerone et al. 1994, 1996, 2000, 2002a, 2002b, 2003; Tagliavini 1999; Marino 1999; Marino et al. 2003). *Tuber* taxa have been distinguished in edible and unedible based on the local use of the ascocarps. The spatial maps have been updated with the 2002–2003 collecting point data of ascocarps used for molecular analyses. Target areas for natural truffle production were identified according to Pavari's phytoclimatic zones (Pavari 1916).

Edible truffle taxa richness has been mapped with DIVA-GIS software (Hijmans et al. 2002) plotting location (points) data (latitude and longitude) in a regional grid with a resolution of 0.1 decimal degrees of latitude and longitude and expressing the “richness” variable as the number of different *Tuber* taxa present in each grid cell (Fig. 3). The geographic distribution of the *Tuber* taxa has been described according to Hodgkin and Guarino (1997) as: (a) common, widely distributed; (b) common, locally distributed; (c) rare, widely distributed; (d) rare, locally distributed.

Based on this partition, a taxon has been considered “common” if more than 10% of its collecting sites were present within at least one phytoclimatic zone; “rare” if the collecting sites were less than 10% within each zone. Taxa are widely distributed if present over at least two phytoclimatic zone or locally distributed if present only in one zone (Table 4).

The spatial distribution of the following 19 *Tuber* taxa was described: *T. aestivum* Vittad., *T. aestivum* fo. *uncinatum* Chatin, *T. borchii* Vittad., *T. brumale* Vittad., *T. brumale* fo. *moschatum* (Ferry) Montecchi & Lazzari, *T. gibbosum* Harkness, *T. magnatum* Pico, *T. macrosporum* Vittad., *T. melanosporum* Vittad. and *T. mesentericum* Vittad. (Fig. 3); *T. excavatum* Vittad., *T. fulgens* Quelet, *T. maculatum* Vittad., *T. oligospermum* Tul. & C. Tul., *T. panniferum* Tul. & C. Tul., *T. regianum* Montecchi & Lazzari, *T. rufum* Pico, *T. rufum* fo. *ferrugineum* (Vittad.) Montecchi & Lazzari and *T. rufum* fo. *nitidum* (Vittad.) Montecchi & Lazzari (Table 4).

Results

Genetic polymorphism

Overall, the nine molecular markers produced 72 PCR fragments. The number of bands detected by a single marker type ranged from 4 to 14, average 8.0, while, molecular weight varied from 0.35 kb to 2.5 kb (Table 2). Marker UBPZ12 detected the highest number of

amplified fragments and (GTG)₅ the fewest (Table 2). On average, RAPD sequences produced more bands (RAPD average=9.5; data not shown) than ITS, or mini and microsatellites. The average value of He by locus was 0.18, ranging from 0.09 (UBPZ23 and (GTG)₅) to 0.28 (UBPZ24) and with the same value for M13 and UBPZ20 (He=0.22) (Table 3). Genetic diversity estimated with Dice's GD, for low values of polymorphism, tended to be quantitatively similar to that evaluated with He (data not shown).

T. aestivum revealed the highest expected intra-specific polymorphism with He=0.30 and a Dice's distance average value between genotypes of DG=0.37, varying from a minimum of 0.02 to a maximum of 0.59. This species was followed by *T. mesentericum* (He=0.21), while *T. brumale* fo. *moschatum* showed the lowest average heterozygosity (He=0.09) (Table 3).

T. magnatum and *T. borchii* revealed similar genetic diversity indices (He=0.16 and 0.17, respectively), both showing a low intra-specific polymorphism. Moreover, within each taxon, individuals with the same geographic origin tended to cluster together, exhibiting a lower genetic diversity (Fig. 2). A correlation between geographic and genetic distances was detected for the genotypes of *T. aestivum* ($r_s=0.32$, $P<0.0001$). The most differentiated genotypes of this species were those from Sirino mount (South-West of Basilicata), which formed a distinct sub-cluster (Fig. 2). The three genotypes of *T. aestivum* fo. *uncinatum*, although sampled in different areas, formed a second sub-group.

Markers SSR (GTG)₅ and ITS1/ITS4 showed a low level of intra-specific diversity per single truffle population, except for *T. aestivum* with He=0.23 and 0.32, respectively (Table 3). Furthermore, *T. magnatum* and *T. brumale* fo. *moschatum* were monomorphic for ITS. In both taxa the most intense amplification products were of about 700 bp in *T. magnatum* and of about 900 bp in the fo. *moschatum*, respectively. The 900 bp fragment was revealed to be specific to *T. brumale* fo. *moschatum*. However a fragment with the same molecular weight was also found in one genotype of *T. mesentericum*. Finally, *T. borchii* mainly produced shorter bands of about 600 bp, except for three genotypes that exhibited fragments of 700 bp, while *T. mesentericum* showed a heterozygote genotype from mount Sirino for ITS locus (figure not shown).

Genetic relationships between taxa

The overall coancestry coefficient was significantly greater than zero ($\theta=0.45$, $P<0.05$) with confidence limits between +0.51 and +0.39 (Table 2, Fig. 2). Theta varied from 0.32 of UBPZ23 to 0.74 of marker SSR (GTG)₅ that was the most useful in differentiating the truffle taxa studied.

The ITS marker was the second most useful molecular tool ($\theta=0.57$), followed by M13 ($\theta=0.43$) and RAPD markers (average $\theta=0.40$; data not shown) in discriminating *Tuber* spp. (Table 2). The ITS 900 bp fragment was the most useful locus in differentiating taxa ($\theta=0.93$) (data not shown).

All ascocarps belonging to the same *Tuber* taxa were grouped together in five sub-clusters which formed two distinctly differentiated groups, the first composed of the closely related white truffles *T. borchii* and *T. magnatum* and the black one *T. brumale* fo. *moschatum*, the second constituted by the other two black species *T. aestivum* and *T. mesentericum* (Fig. 2). The first cluster was more differentiated than the second, and *T. brumale* fo. *moschatum* was the most differentiated taxon among the *Tuber* entities studied. Within the second group, *T. mesentericum* was more differentiated than *T. aestivum*. Finally, two private alleles were detected in *T. aestivum* by two different RAPD sequences: a fragment of 800 bp (UBPZ206) and a band of 350 bp (UBPZ23) with

Table 3 Expected heterozygosity (He) per locus, per population and private alleles detected within the 6 studied *Tuber* taxa

| Species and forms | Expected heterozygosity (He) | | | | | | All molecular markers | Private alleles (frequency) |
|--------------------------------------------|------------------------------|------|--------------------|--------|--------|--------|-----------------------|-----------------------------|
| | ITS1/ITS4 | M13 | (GTG) ₅ | UBPZ12 | UBPZ23 | UBPZ20 | | |
| <i>Tuber aestivum</i> | 0.32 | 0.37 | 0.23 | 0.31 | 0.13 | 0.37 | 0.35 | 0.26 |
| <i>Tuber mesentericum</i> | 0.18 | 0.29 | 0.04 | 0.23 | 0.08 | 0.26 | 0.12 | 0.37 |
| <i>Tuber borchii</i> | 0.13 | 0.20 | 0.10 | 0.13 | 0.06 | 0.25 | 0.08 | 0.30 |
| <i>Tuber magnatum</i> | 0.00 | 0.25 | 0.12 | 0.19 | 0.14 | 0.13 | 0.21 | 0.08 |
| <i>Tuber brumale</i> fo. <i>moschatum</i> | 0.00 | 0.12 | 0.03 | 0.05 | 0.04 | 0.19 | 0.01 | 0.29 |
| <i>Tuber aestivum</i> fo. <i>uncinatum</i> | 0.11 | 0.09 | 0.00 | 0.19 | 0.11 | 0.12 | 0.06 | 0.33 |
| Average values | 0.12 | 0.22 | 0.09 | 0.18 | 0.09 | 0.22 | 0.14 | 0.28 |
| | | | | | | | 0.19 | 0.18 |

a frequency of 46 and 14%, respectively, while a third private allele of 400 bp (UBPZ24) with a frequency of 87%, was found in *T. borchii* (Table 3).

Ecogeographic distribution

In terms of geographical distribution, the following edible taxa were common and widely distributed (CW): *T. aestivum*, *T. mesentericum*, *T. aestivum* fo. *uncinatum*, (Table 4). *T. borchii* and *T. magnatum* turned out common and locally distributed (CL), while *T. brumale*, *T. brumale* fo. *moschatum*, *T. gibbosum* and *T. macrosporum*, were rare and widely distributed (RW). *T. melanosporum* resulted rare and locally distributed (RL) (Table 4). The geographical distribution of unedible taxa is affected by the bias due to the sampling driving force. As the unedible taxa were sampled only for research purposes, it is likely that taxa reported as rare and locally distributed (Table 4) vice versa are more common and more widely distributed.

Edible *Tuber* species mainly grow on the western Apennine side of the Basilicata region (Fig. 3). Collecting sites of edible truffles are spread over the cold *Lauretum* (146 localities) and *Castanetum* (122 localities) phytoclimatic zones (Table 4), both of which are characterised by climatic and ecological conditions suitable to truffle growth and reproduction.

Table 4 Geographical distribution and ecological relationships assessed in terms of number of collecting sites per taxa within each phytoclimatic Pavari's zone

| Species and forms | Geographical distribution ^a | Collecting sites (No.) | | | | | |
|-----------------------------------------|----------------------------------------|------------------------|--------------|------|--------------------|----|-----|
| | | Lauretum sub-zones | | | Castanetum Fagetum | | All |
| | | Warm | Intermediate | Cold | | | |
| Edible | | | | | | | |
| <i>T. aestivum</i> | CW | 2 | 8 | 39 | 33 | 11 | 93 |
| <i>T. mesentericum</i> | CW | 1 | 5 | 25 | 24 | 8 | 63 |
| <i>T. aestivum</i> fo. <i>uncinatum</i> | CW | 0 | 4 | 26 | 22 | 7 | 59 |
| <i>T. borchii</i> | CL | 3 | 6 | 13 | 9 | 1 | 32 |
| <i>T. magnatum</i> | CL | 2 | 7 | 16 | 9 | 1 | 35 |
| <i>T. brumale</i> | RW | 0 | 3 | 11 | 8 | 2 | 24 |
| <i>T. brumale</i> fo. <i>moschatum</i> | RW | 0 | 1 | 3 | 3 | 1 | 8 |
| <i>T. gibbosum</i> | RW | 0 | 2 | 6 | 4 | 2 | 14 |
| <i>T. macrosporum</i> | RW | 0 | 0 | 2 | 8 | 3 | 13 |
| <i>T. melanosporum</i> | RL | 0 | 2 | 5 | 2 | 0 | 9 |
| All | | 8 | 38 | 146 | 122 | 36 | 350 |
| Unedible | | | | | | | |
| <i>T. rufum</i> | CW | 0 | 1 | 5 | 4 | 1 | 11 |
| <i>T. excavatum</i> | CW | 0 | 1 | 6 | 2 | 1 | 10 |
| <i>T. rufum</i> fo. <i>nitidum</i> | CL | 0 | 1 | 1 | 2 | 0 | 4 |
| <i>T. regianum</i> | CL | 0 | 0 | 0 | 2 | 1 | 3 |
| <i>T. panniferum</i> | RL | 0 | 1 | 0 | 1 | 0 | 2 |
| <i>T. fulgens</i> | RL | 0 | 0 | 1 | 0 | 0 | 1 |
| <i>T. maculatum</i> | RL | 0 | 0 | 0 | 1 | 0 | 1 |
| <i>T. oligospermum</i> | RL | 1 | 0 | 0 | 0 | 0 | 1 |
| <i>T. rufum</i> fo. <i>ferrugineum</i> | RL | 0 | 0 | 0 | 0 | 1 | 1 |
| All | | 1 | 4 | 13 | 12 | 4 | 34 |

^aC, common (>10% of collecting sites within at least one zone); R, rare; W, widely distributed (presence of collecting sites over each of the three zones); L, locally distributed

Tuber aestivum was the most common and widely distributed truffle at regional scale, spanning from lowland zones up to the western Apennine belt (Table 4).

T. mesentericum, the second widely distributed species, as *T. aestivum*, was evenly distributed over the three main Pavari's zones, mainly in centre-western areas and from lower altitudes to 1000 m (Table 4). It was often in symbiosis with *Fagus sylvatica* L. and in sympatry with *T. aestivum* fo. *uncinatum* in calcareous soils, rich in organic matter.

T. borchii was common and locally distributed on the western side and in pine forests (*Pinus* spp.) of the Ionian coast, while few collecting sites of unmarketable and morphologically similar *T. gibbosum* were localised on the eastern side in Pavari's *Lauretum* cold sub-zone and *Castanetum*, always in symbiosis with *Pseudotzuga menziesii* Mirbel. an introduced North American conifer (Table 4).

T. brumale showed almost the same geographic distribution as *T. aestivum* and *T. aestivum* fo. *uncinatum*, growing in well-drained and also stony soils.

While *T. brumale* fo. *moschatum* revealed an ecogeographic distribution almost coincident with that of the morphologically similar *T. brumale* but it was found also in a lower number of localities. Several ascromata of *T. magnatum* were common in a wide natural site of the Sinni catchment basin (at 300 m), toward the intermediate and cold *Lauretum* Pollino National Park sub-zones and in symbiosis with grey poplar (*Populus canescens* Aiton). *T. magnatum*, although common and locally distributed at a regional level, is evenly distributed across different phytoclimatic zones at a sub-regional level (Table 4). This pattern of distribution is mainly due to its host species (*Populus* spp. and *Salix* spp.) that are pioneer species, forming corridors along the minor and major drainage lines.

The richness of edible taxa ranged from 6 to 9 different taxa in three sub-regions (three black grid cells in Fig. 3). Pollino National Park turned out to be particularly rich in both edible and unedible truffles. The pedological structure (unstable slopes and prevalence of clayey deposits) associated with scarce rainfall and snow (<700 mm/year), higher temperatures (more stringent Mediterranean climate) and a reduced forest landcover, make the eastern side of the region unsuitable for truffle growth. Almost all taxa of *Tuber*, preferred permeable calcareous and sedimentary soils of the western areas of Basilicata, whereas *T. magnatum* mainly preferred the well drained tertiary marly, clayey and sandy fluvial deposits.

Discussion

The results of this study confirm that the Basilicata region, as a consequence of its environmental heterogeneity, is particularly rich in *Tuber* taxa as characterised by genetic diversity. Molecular markers used to evaluate *Tuber* genetic diversity, exhibited different properties in assessing genetic variation. Overall the used markers were useful tools for monitoring the intra and interspecific polymorphisms, clearly differentiating *Tuber* taxa and evaluating their genetic and phylogenetic relationships. The genetic differentiation estimates are in agreement with what has been observed for autogamous plants (Loveless and Hamrick 1984; Nei 1987; Figliuolo and Perrino 2004). Thus molecular data significantly discriminated the *Tuber* taxa, a priori defined with morphological characters, showing the existence of a consistency between the phenotypic descriptors and the genetic ones.

However, according to Grechko (2002), data obtained using different classes of molecular markers should be combined to reduce the errors in assessing genetic relationships among taxa.

According to Longato and Bonfante (1997) and Mello et al. (2002), marker SSR (GTG)₅ was not suitable to evaluate intra-specific genetic variability but showed the greatest aptitude to differentiate *Tuber* species. ITS1/ITS4 partly distinguished *T. brumale* fo. *moschatum* from all remaining *Tuber* taxa except for one genotype of *T. mesentericum* that showed the same pattern of forma *moschatum*. Thus, some authors designed species-specific ITS primers (Amicucci et al. 1998; Rubini et al. 1998) or used a combination of PCR-ITS and restriction enzymes to obtain diagnostic patterns and discriminate among closely related truffles (Paolocci et al. 1997; Bertini et al. 1998, 1999).

Species-specific fragments were also selected for RAPD markers to design diagnostic pairs of primers or probes (Amicucci et al. 1997; Rossi et al. 2000). However, because the aim of this study was to investigate regional *Tuber* biodiversity, different types of molecular markers were better for testing of truffle genome.

Also RAPD loci employed in this research, with the only exception of UBPZ23 (that showed both the least value of coancestry coefficient and a low aptitude to detect intra-specific polymorphism), detected polymorphisms among the truffles studied and demonstrated genetic relationships between them according to Gandeboeuf et al. (1997). Finally, minisatellites M13 were useful to show within taxon variation (high value of He by locus).

Moreover, the low level of intra-specific polymorphism computed with SSR (GTG)₅ and ITS in *T. magnatum* and in *T. borchii*, both of which were sampled in single regional sites (the Pollino National Park and the Ionian coast area, respectively), also confirms the results of Mello et al. (2002) and Longato and Bonfante (1997) who found a high level of Dice Genetic Similarity ($S=0.90$) for isolates of these two species from Central Italy. In addition, results obtained for *T. magnatum* agree with those of Rubini et al. (2004) who detected an average expected heterozygosity of 0.17 for samples from the Basilicata, their most southern collecting site. These data confirm that populations of *T. magnatum* from southern Italy are characterised by a lower genetic diversity. As genetic diversity in *T. aestivum* is twice as great, and in *T. mesentericum* is intermediate (Pacioni and Pomponi 1991; Mello et al. 2002; Weden et al. 2004).

T. aestivum showed a good adaptability to different pedoclimatic conditions and a higher resistance to dryness in respect to other black truffles as *T. brumale* and *T. melanosporum*.

Moreover the lower genetic diversity among ascocarps of *T. aestivum* from the same origin and the significant isolation by distance (correlation between matrices of genetic and geographical distances), suggest that it is possible to investigate the population genetic structure of each *Tuber* species using a more representative sampling. The high number of alleles observed in *T. aestivum* could be due to its greater effective population size maintained during the last glaciation, given that this species ripens in spring and summer and thus escapes the low temperature effects. This glaciation hypothesis could explain also low genetic diversity observed in *T. melanosporum* (Bertault et al. 1998, 2001). The three genotypes of *T. aestivum* fo. *uncinatum* constitute a distinct sub-group within the *T. aestivum* sub-cluster, but, based on the phylogenetic concept of species, it is not possible to consider this a priori defined taxon as a different species.

Finally, from a taxonomic point of view, relationships detected among *Tuber* taxa were also consistent with results of Mello et al. (2002), confirming a genetic similarity between the two species of black truffle, *T. aestivum* and *T. mesentericum* and the two white ones *T. borchii* and *T. magnatum*, while *T. brumale* fo. *moschatum* demonstrated to be more closely related to the group of white truffles than to the other black taxa.

In conclusion, the richness in *Tuber* spp. of the Basilicata region and the existence of geographic patterns of genetic variability suggest that several differentiated ecogeographical

areas of the Basilicata could be proposed as gene-reserve either for edible or unedible truffles. The most suitable zones for this goal are mainly located along the Apennine belt, on the western side of the region (such as Sirino and Pollino mounts), but some collecting sites, often of the less common or unedible taxa, are located also in its hilly eastern areas, along rivers and along the Ionian coast. The intermediate and cold *Lauretum* Pollino National Park sub-zones can be considered one of the most southern natural stations of *T. magnatum* detected so far in Europe (Marino 1999; Cerone et al. 2002a). Previous studies on its natural sites referred mainly to northern and central Italy (Montacchini and Caramiello 1968; Bencivenga and Granetti 1990; Tocci et al. 1995; Amicucci et al. 1997; Bencivenga 1998).

The evaluation of molecular variation of this valuable germplasm and the monitoring of genetic diversity represent important ways for planning in situ conservation strategies, particularly for truffles at high risk of extinction such as the main species protected by the Italian Law No. 752/85. In addition, the study of inter- and intra-specific variability allows a better understanding of spatial phylogenesis of these hypogeous fungi. A more detailed study of population (species) molecular variation, based on a representative sampling at inter-regional level (South versus North), should be necessary to validate recent models of dynamics and spatial genetic diversity of truffles (Bertault et al. 1998, 2001; Murat et al. 2004).

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Multi-scale analysis of butterfly diversity in a Mediterranean mountain landscape: mapping and evaluation of community vulnerability

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Abstract This paper is an attempt to outline a protocol for animal diversity census and evaluation aimed for areas in view of landscape planning of territories of hundred square kilometres and more, that may work utilising different faunal groups and be anyway useful at various scales. Many papers are addressed to elaborate tools for landscape planning starting from biodiversity evaluation and butterflies are often utilised because of their sensitivity to landscape modifications. In this work, the biodiversity evaluation has been performed using three hierarchically linked landscape units at micro-, meso- and macro-scale. Being species diversity values often inadequate to define the conservation interest of a landscape portion, more importance has been given to which species compose the species assemblages. A community vulnerability Index was coded and used for evaluating potential consequences of human disturbance on butterfly assemblages. Forty-four year samples were gained by visual census in the Sila Greca, Southern Italy, on an area of approximately 520 square kilometres. During 5 years work, 2,535 specimens and 94 species were recorded, equal to 75.8% of the whole Calabrian fauna. Four vulnerability levels have been established and used for mapping butterfly assemblage vulnerability in the area, starting from a vegetation map. Species richness was found somewhat contradictory at micro-scale, where the community vulnerability Index gives a sounder approach. *S* diversity gives a more reliable picture of naturalness at meso-scale, a level we identified with the “ecotope”. At this more “geomorphic” scale level, biological functions reflected by butterfly assemblages revealed to be clearly linked to seral processes. Similarity analysis results show that the ecotope species richness, here called “eta-diversity”, could be an useful measure of zoological landscape (faunation) potentialities.

Keywords Butterflies · Diversity · Species assemblages · Vulnerability · Landscape scale · Ecotope · Eta-diversity · Landscape planning

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Introduction

A large body of literature is addressed to elaborate practical tools for applying results of biological research in conservation of natural resources and landscape planning, but in many cases at least two problems make these tools inapplicable: (1) their relevance limited to a single taxon and (2) the difficulty to link results to functional landscape units. Papers devoted to conservation topics often utilise biodiversity as a tool for investigating and evaluating the interest of an area (Magurran 1988; Gaston 1996; Conroy and Noon 1996; Myers et al. 2000) but it is at least similarly important to take into account ecological attributes of surveyed species assemblages (Kremen 1992). Diversity values per se, whether S or other diversity indices, are often inadequate to define the conservation interest of a given landscape portion (Samways 1994). Intensification of human activities, in fact, does not always lead to a decrease in species richness (Burel et al. 1998), depending on the faunistic group surveyed and the intensity of environmental alterations (Blair and Launer 1997). Starting from such premises, it becomes important to evaluate which species compose species assemblages, and the abundance they have, for carrying out correct conclusions (Kremen 1992). In this address, the evaluation of life history traits of species could be very useful.

Several studies suggest that many faunal higher taxa may be used as surrogates and correlates of biodiversity (Noss 1990; Duelli and Obrist 1998; Blair 1999), but each taxonomic group has its own ecological features representing just a small functional portion of an ecosystem. Indeed many papers involving more than one taxon are available (e.g. Blair 1999; Söderström et al. 2001; Kruess and Tscharntke 2002; Jeanneret et al. 2003). Instead of a multi-taxa approach, a mono-taxon approach could be utilised in areas monitoring and conservation studies when correctly chosen and utilised (Kremen 1992). Butterflies were often used as bioindicators because they play important ecological roles as herbivores, pollinators and prey, and are known to be strictly correlated to habitat diversity (e.g. New 1991; Pollard and Yates 1993; Molina and Palma 1996; Blair and Launer 1997).

In order to avoid mistakes in ranking priority areas for conservation, it is necessary to link the results to a functional landscape unit. Lapin and Barnes (1995) suggest a landscape ecosystem approach to assess and map plant and ecosystem diversity. This approach, partially followed here, is an attempt towards the individuation of nonarbitrary and functional units in landscape ecology studies and diversity mapping, but the ecosystem concept is unlinked to spatial scales.

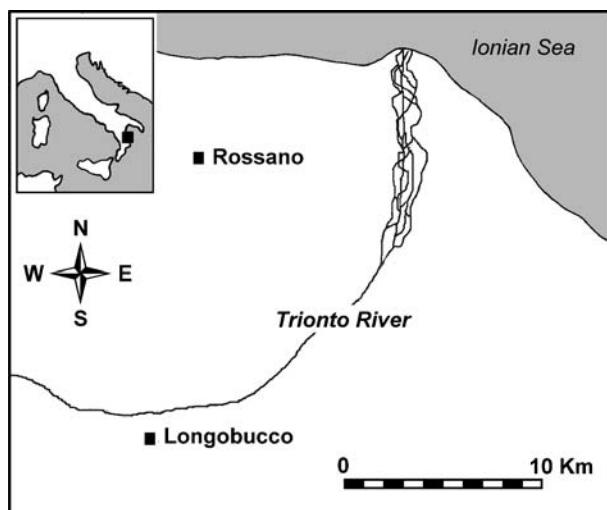
In this paper, we used a hierarchically nested approach in evaluation the diversity and the vulnerability of butterfly communities. Data registered at micro-scale, i.e. within surveyed sites, were used to obtain data at meso-scale and macro-scale following a bottom-up strategy. In this way, we hoped (1) to evaluate the consequences of human activities on butterfly assemblages at various scales, and (2) to build a cartographic model of diversity. A multi-scale approach in diversity studies is very important because diversity patterns depend on different factors at various scales. In short, the purpose of this paper is to produce a useful framework for landscape managing and territorial planning whatever the surface of given territory and that works involving indifferently many faunal groups or “guilds”.

Methods

Study area

Surveys were carried out in the Sila Greca Massif (Fig. 1), Calabria, Southern Italy. The study area reaches a maximum height of 1,635 m a.s.l. on a surface of about 520 km² and

Fig. 1 Location of the Sila Greca Massif on the Ionian coast of Calabria, Southern Italy



is marked by a long dry season from May until September, that becomes shorter with the increase of altitude. Geologically, the territory may be subdivided in three zones. The mountain zone (above 600 m a.s.l.) is mainly granitic or dioritic and it is characterised by an irregular topography and deep ravines. The hilly zone (100–600 m a.s.l.), metamorphic or sedimentary, has a sweetly undulating morphology interrupted by rocky slopes and by large river beds filled by gravels, locally called “fiumare”. The coastal lowland (0–100 m a.s.l.), shows a pedogenetic substratum composed by marls, pliocenic or oligocenic clays and quaternary alluvium.

Usually, in conservation studies focused on faunistic species assemblages, sampling effort was done on territorial surfaces smaller than in this study (e.g. Ricketts et al. 2001: 227 ha; Simonson et al. 2001: 754 ha; Jeanneret et al. 2003: 8 km²; this study: 520 km²) because of difficulties in data collection and mapping.

The vegetation of Sila Greca (Bernardo et al. 1991) belongs to two biomes: the sclerophylls, dominated by the holly oak (*Quercus ilex* Linnaeus, from sea level until 500 m a.s.l.), and the deciduous temperate forests given by a lower oak belt (warmer, with more *Quercus* species and the chestnut *Castanea sativa* Miller largely widespread, from 500 until 1,100 m a.s.l.), and above 1,100 m a.s.l., a “subatlantic” beech belt with *Fagus sylvatica* Linnaeus forests intermingled with *Pinus laricio* Poiret “paraclimax” stands,

In this paper, we propose a hierarchical, spatially nested experimental design. Three hierarchically linked landscape layers for biodiversity evaluation are chosen: (i) the micro-scale landscape unit (micro-LU) (from less than 0.1 to 10 ha), corresponding to surveyed sites; (ii) the meso-scale landscape unit (meso-LU) (from 1 to 10,000 ha), corresponding to a landscape unit marked by the same vegetation potentialities and identified mostly on geomorphological bases; (iii) the macro-scale landscape unit (macro-LU) (from 1,000 to 100,000 ha and more), corresponding to a large portion of a geographical region, here the whole study area. Biodiversity of higher layers will be obtained adding data collected within its lower layers. Forty-four sites representative of the main ecological successions and of the more important man-made biotopes present in the Sila Greca territory were chosen (Table 1). The number of surveyed sites, i.e. the sampling effort, has been

Table 1 Sample sites list

| Name | Meso-LU | m a.s.l. | % | LU | Name | Meso-LU | m a.s.l. | % | LU |
|--------|---------|----------|-----|-------------|-------|---------|----------|----|---------------|
| *Tdun1 | SCD | 3 | 0 | Meadow | TLe4 | MH | 580 | 75 | Wood |
| *TLS1 | LH | 40 | 0 | Meadow | TLe5 | MH | 580 | 60 | Clearing |
| *TU11 | LH | 65 | 35 | Olive-grove | TPi1 | MH | 590 | 65 | Reforestation |
| *TP1 | LH | 100 | 0 | Pasture | TTe | R | 470 | 0 | Pasture |
| *TEu1 | LH | 160 | 60 | Reforest. | TCa | HH | 550 | 65 | Wood |
| TP2 | LH | 215 | 0 | Pasture | Teuf1 | HH | 565 | 5 | Pasture |
| RP2 | AF | 340 | 0 | Pasture | TPr1 | HH | 570 | 5 | Pasture |
| TAg | AF | 560 | 85 | Wood | TQ1 | HH | 575 | 80 | Wood |
| *THe1 | F | 75 | 0 | Garigue | TCe1 | HH | 820 | 80 | Wood |
| *TN01 | F | 75 | 60 | Wood | TCa2 | HH | 850 | 75 | Wood |
| *TN02 | F | 80 | 75 | Wood | TCa1 | HH | 890 | 90 | Wood |
| *THe2 | F | 90 | 0 | Garigue | TCe2 | HH | 1,090 | 75 | Wood |
| *TN03 | F | 90 | 90 | Wood | TPi2 | M | 1,005 | 35 | Clearing |
| TLe1 | MH | 180 | 90 | Maquis | TAf | M | 1,165 | 60 | Wood |
| TLe2 | MH | 350 | 90 | Maquis | SPr1 | M | 1,550 | 0 | Clearing |
| RP1 | MH | 360 | 5 | Clearing | SPi2 | M | 1,570 | 45 | Wood |
| RLe1 | MH | 365 | 100 | Maquis | SRad1 | M | 1,630 | 10 | Clearing |
| RColl1 | MH | 380 | 0 | Cultivation | SFag1 | M | 1,635 | 80 | Wood |
| RQ1 | MH | 400 | 50 | Wood | TAq | TS | 1,150 | 85 | Wood |
| TLe3 | MH | 400 | 95 | Maquis | TAq1 | TS | 1,155 | 25 | Clearing |
| TCi1 | MH | 530 | 85 | Maquis | TP3 | H | 1,100 | 0 | Cultivation |
| TLed | MH | 540 | 30 | Maquis | TGin1 | H | 1,270 | 40 | Maquis |

Sites are identified by alphanumerical sequences (Name). For each of them are reported: meso-scale landscape unit of appurtenance (Meso-LU); altitude (m a.s.l.); percentage of tree/bush cover (%); Land use category (LU). Sites marked * were surveyed on two separate years

proportionally subdivided among meso-LUs looking at their surface in the study area (Table 2). Sample sites were not randomly chosen, because both random sampling design and stratified random sampling design were inapplicable. The dense landscape fragmentation of the Sila Greca Massif could have lead to the census exclusion of some particular habitat from surveyed sites, and the very hard topography of the Massif made the access at random places very difficult and time consuming. Main meso-LUs were identified by taking into account (a) geological substrata, (b) geomorphic features, and (c) climate conditioned vegetation (see Table 2). Meso-LUs may be “zonal” or “azonal”: in zonal meso-LU series run up to the final stage of the ecosystem determined by climate (the climax, in Europe mostly a forest), in azonal ones the bedrock and other physical conditions as subsoil water or erosion, restrain the development of ecosystem/vegetation to early succession stages (sand dunes, river beds, rock cliffs, etc.).

Sampling

Field work was carried out from 1993 to 1998 by investigating new sample sites each year. Sample sites were each third week monitored from March until November, in sunny days and between 9:30 a.m. and 3:00 p.m., inverting daily sequence of visits. If the first sampling sequence of sample sites was ABC, the second was CBA, the third ABC and so on, reducing on this way the sampling hour effects on collected data. A zigzag line was followed during systematic walking surveys, 10 min long to limit the ingress of individuals into the sample site. No one point of sample sites was covered more than once. A time constrained sample has been chosen instead a surface constrained sample because of

Table 2 List and short description of meso-scale landscape units (Meso-LU) of the Sila Greca

| Meso-LU | Average altitude (m a.s.l.) | Geomorphological features | Dominant vegetation at climax stage* | % in the Sila Greca Massif | Sample sites |
|---------------------------|--------------------------------|---------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------|-------------------------------|-----------------|
| Azonal | | | | | |
| Sandy Coastal Dunes (SCD) | 3 | Sandy substratum | Halophilic plants | <1% | 1 |
| Fiumara (F) | 80 | Illogical substratum with gravels and sand of various dimension, scarce in humus and very variable water flow | <i>Tamarix</i> sp. pl., <i>Nerium oleander</i> Linnaeus, <i>Helichrysum italicum</i> (Roth) Don. | ≤5% | 5 |
| River (R) | 470 | Alluvial substratum with medium size sediments, low humus level and constant water flow | <i>Salix</i> sp. pl. | <1% | 1 |
| Alluvial Fans (AF) | 450 | Alluvial substratum with sediments of small dimension, rich in humus and constant water flow | <i>Alnus</i> sp. pl. | <1% | 2 |
| Talus Slopes (TS) | 1,150 | Incoherent substratum composed by stones and rock debris | Azonal sparse vegetation | <1% | 2 |
| Low Hill (LH) | 120 | Clay substratum, sweet moulded or gentle topography, heavy soilfuction and “calanchi” bad lands | <i>Pistacia lentiscus</i> Linnaeus, <i>mediterranean sclerophyll forest</i> | ≥20% | 5 |
| Zonal | | | | | |
| Medium Hill (MH) | 450 | Metamorphic, granitic or calcareous substratum, irregular topography | Sclerophyll forest | ≥28% | 12 |
| High Hill (HH) | 700 | Metamorphic or granitic substratum, very irregular topography | <i>Quercus</i> sp. pl., <i>Castanea sativa</i> Miller | ≥22% | 8 |
| Mountain (M) | 1,400 | Granitic substratum | <i>Fagus sylvatica</i> Linnaeus, <i>Pinus laricio</i> Poiret | ≥13% | 6 |
| Highlands (H) | 1,150 | Alluvial substratum with sandy sediments. Upper part of the Sila Greca Upland | <i>Pinus laricio</i> Poiret | ≥8% | 2 |

*Not modified by man, pristine

difficulties to find biotopes sufficiently large and homogeneous for diluting discontinuity in the distribution of populations.

In order to estimate population changes and influence of chance on results ten sites (see Table 1) were surveyed on two separate years, while, in order to know community modifications during the day, a pasture (TP1) was surveyed at 9:00/10:00 a.m., 12:00/1:00 p.m., 2:00/3:00 p.m.

Individuals found at boundary of stands are not registered. Specimens were identified in the field and immediately released. The species were named according to Balletto and Cassulo (1995).

Data analysis

A species/sample sites matrix (MS/S) constructed by using the registered individual number (N), was the data source for any further analysis. Qualitative (QS) and quantitative percentage (PS) similarity indices were used to compare species assemblages (see Hanski and Koskela 1977). The qualitative similarity index is a binary measure based on presence/absence data, $QS=2c/(a+b)$, in which c equals the number of species present in both samples, a equals the number of species present in sample 1, b equals the number of species present in sample 2 (Sørensen 1948). The percentage similarity index is based on the coverage of a species in a sample, $PS=\Sigma \min(p_{i1}, p_{i2})$, in which p_{i1} equals the proportion of species i in sample 1, and p_{i2} equals the proportion of species i in sample 2 (Renkonen 1938). Both index values were expressed in percentages.

The Canonical Correspondence Analysis (CCA) was carried out by using STATISTICA 5.5 (StatSoft Italia 1999). This constrained ordination technique permits to individuate “*a posteriori*” which environmental parameters drive species distributions. Environmental variables are theoretically identified with the extracted dimensions (D) (or axis) by using species ecology and variables of surveyed sites. An inertia value, associated to each dimension, explains the percentage of the total variance in species distribution attributable to each dimension.

Spearman rank correlation (r_s) and Pearson correlation (r_p) was computed by Systat version 9.0 (SPSS 1998).

Main life history traits of species were taken into account. In particular, mobility ranges and fundamental ecological categories proposed by Balletto and Kudrna (1985), partly modified because of the different habitat affinity shown by some species in Calabria, were considered the most important life history traits from a conservation viewpoint (Scalercio 2002). Mobility range (MR) vary from 1 for sedentary species to 5 for migrant species. Species have been assigned to the following fundamental ecological categories: mesophilous (M), thermophilous (T), eurytopic (E), sciophilous (S), xerophilous (X).

Diversity analysis were performed by using ESTIMATES5 (Colwell 1997). Species richness (S), Shannon's index (H') and Simpson's index (λ) were chosen as diversity measures. We selected Shannon's and Simpson's indices because relatively easy to interpret ecologically, widely used and less sensitive to rare species and sample sizes (Magurran 1988). The same program estimated total species richness of study area (for complete list and explanation of estimate indices see Colwell (1997)) and constructed rarefaction curves (species/sample sites and species/individuals) after 50 sample randomisations.

In order to evaluate landscape naturalness, we computed a community vulnerability Index (I_v) integrating information from Shannon's index (H') with some autoecological parameters, linking descriptive to functional data. First, it is important to valuate responses

of species to human activities. Indeed, communities may be composed mainly by highly mobile species (capable to escape consequences of environment alterations), or by eurytopic species (capable to adapt to live in contiguous biotopes). Species mobility is an important measure of species vulnerability as underlined in Pollard and Yates (1993). Mobility (M) and eurytopic (E) of communities were computed on the basis of species contributes as follows:

$$M = \Sigma(p_i \text{MR}_i)$$

where:

p_i is proportion of individuals of the species i in the assemblage;

MR_i is mobility range of species i

$$E = \Sigma P_e$$

where P_e is proportion of individuals of eurytopic species in the assemblage.

In conclusion, we propose the following equation:

$$I_v = (H'/M) - 2E$$

where:

I_v is community vulnerability Index

H' is Shannon's index value of species assemblage

M is mobility of species assemblage

E is eurytopic of species assemblage

In this equation the importance of eurytopic species was emphasized, because they may take greater benefits from human activities than species having high mobility.

Results

Reliability of collected data

Different year samples of the same stand show similarity patterns variable from 14.3% to 76.5%. Both similarity indices are positively correlated with numbers of individuals collected in each sample site (QS : $r_s = 0.66$, $n = 10$, $p = 0.019$; PS : $r_s = 0.74$, $n=10$, $p=0.07$). In “pseudo-communities” composed by few specimens, collected data are strongly influenced by chance, while assemblages marked by high abundance values show more durable and characteristic species structures. As a consequence, species assemblages composed by few individuals have a low reliability and all conclusions about them have no real statistical significance.

TP1 species assemblages monitored at various times of the day, show well-defined patterns. Morning samples are the most abundant and rich ($S = 8$, $H' = 2.79$); just one species, *Polyommatus icarus*, was found three times; the 50% of species ($S_{\text{tot}}=12$) were found at least twice. Taxa found only once attain low abundance values (no more than three individuals) belonging to the species assemblage tail.

Rarefaction curves of sample sites and individuals have shown that one half of the sample sites was sufficient to collect $87.6 \pm 3.8\%$ of species, while sampling half of the

individuals is sufficient to find $88 \pm 3.7\%$ of species (both with 95% of confidence limits, c.l.). Estimated species richness of the whole study area should be comprised between 98 and 111 species, depending on estimates by different indices (see Colwell 1997).

Main determinants of butterfly species assemblages

The CCA shows that the first seven dimensions are necessary to explain the 50.7% of total inertia, according to the high number of variables playing a role in a so large territory and during a so long field research. The analysis of macro-ecological parameters of surveyed sites shows that the most explicative dimension (D1) (10.16% of inertia) discriminates according to tree/bush cover ($r_p = -0.45, p = 0.002$). Usually, in an ecological study performed in a very large territory, extended from the sea level to the mountain top, the altitude explains the largest part of inertia. Here the altitude gradient is identifiable with D3 (8.74% of inertia) ($r_p = -0.87, p < 0.0001$). Two small riparian woods (TN02 and TN03) and a maquis with high bush cover (TCi1), are positioned among meadows and pastures on D1 because of the shelter offered to meadow-dwelling species during the hottest months. During the summer, these woods provide an acceptable microclimate for butterflies (refuge-effect). The importance of vegetation structure in providing insects with microclimate variations was discussed by Strong et al. (1984). A mountain maquis (TGin1) and a mountain pasture (TP3) settle in an unexpected way along D3, because of the continental climate and high soil permeability of the Sila Greca Upland. These stands give hospitality to thermophilous species typical of low altitudes. In consequence, *Hipparchia semele* and *Polyommatus dorylas*, usually present at high altitude in Southern Italy and sampled within these stands, show D3 values similar to Mediterranean species.

Effects of environmental structure (as cover percentage) on species assemblages may be analysed by subdividing sample sites into three groups having different percentage of tree/bush cover: herbaceous micro-LUs (0–14%), ecotonal micro-LUs (15–74%), and forest micro-LUs (75–100%). Average percentage similarity values (PS) carried out from the comparison-pairs of herbaceous micro-LUs are higher (32.7%; SD = 14.5) than in forest ones (17.3%; SD = 13), attaining intermediate values in ecotonal ones (23.6%; SD = 12.6).

Diversity at macro-scale

Eight families, 94 species and 2,535 specimens were registered in the Sila Greca Massif. The complete list of species was reported in Scalercio (2002). The 75.8% of the whole Calabrian fauna was recorded. Species richness is significantly related to the number of individuals ($r_p = 0.83, p < 0.0001$). No species occurred in all 44 sites, while 15 species occurred in only one sample site.

The nine most abundant species are sufficient to attain the 50% of sample. *Polyommatus icarus* (12.3% of individuals versus the 75% of the sites), and *Pieris rapae* (10.8% of individuals vs. 86.4% of sites) are the most abundant and widespread butterflies. Both are sinanthropic, favoured by human activities.

Diversity at meso-scale

A map model of the Sila Greca meso-LUs has been drawn by emphasizing their species richness values (Figs. 2a, 3). Sandy Coastal Dunes (SCD) ($S = 18$) and Fiumara (F)

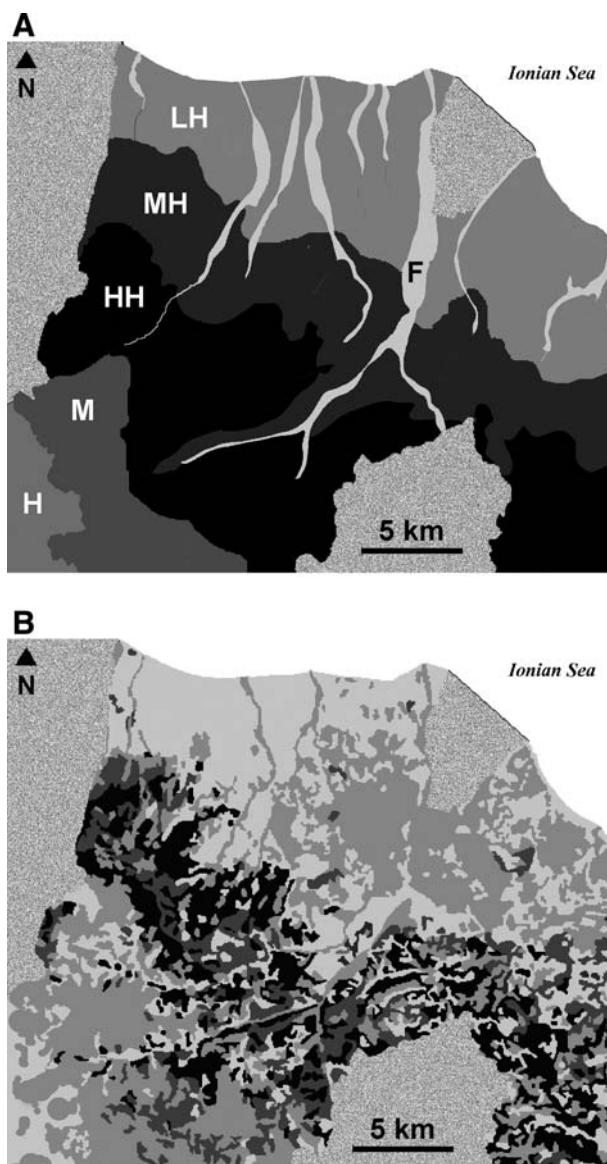


Fig. 2 (A) Cartographic model of the Sila Greca meso-scale landscape units. Small landscape units (less than 1% of study area) are not represented. The increasing grey scale corresponds to increasing species richness. (B) Map of the community vulnerability Index (I_v). Note the importance of Mediterranean rivers ("fiumare"), at low altitude. The increasing grey scale corresponds to increasing I_v values

($S = 18$) lodge the lowest species richness, Medium Hills (MH) ($S = 50$) and High Hills (HH) ($S = 55$) contain the highest ones. This could be explained by the paleo-biogeographical history of Calabria, starting the presence of some species in the Sila Greca Massif from the last glaciation. These taxa are now present mainly in Mountain (M) ($S = 44$), but they can penetrate lower altitude landscapes by exploiting microclimate conditions of the deep valleys and ravines. Other meso-LUs have species richness values

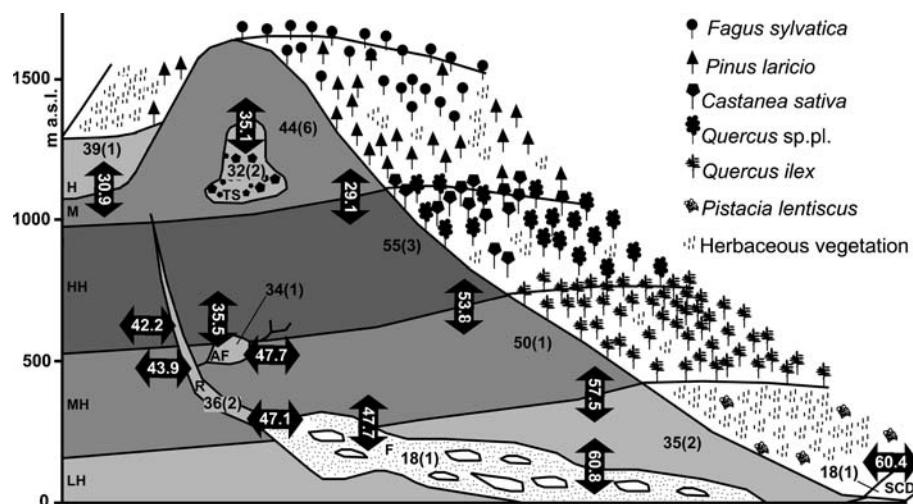


Fig. 3 Model of the Sila Greca territory reporting meso-LUs, their schematic vegetal cover and their main data. Double-arrows: percentage similarity (PS) between contiguous meso-LUs; black numbers: species richness and (unique species). The increasing grey scale corresponds to increasing species richness

comprised between 32 and 44. The comparison of hills shows the Lower Hill (LH) ($S = 35$) poorer in species than other hill meso-LUs. All the ten recognised meso-LUs bear at least one unique species ($S_u = 3$), but in many cases because of stochastic reasons. Just within High Hill ($S_u = 3$), the least man modified, and within Mountain ($S_u = 6$), because of its above remembered paleo-biogeographical history, the unique species are significantly more numerous.

Medium Hill and High Hill share the most species (Table 3). A number of mesophilous elements are shared by these meso-LUs because their climax ecosystem stages are both deciduous forest, which create similar abiotic conditions. The least similar meso-LUs are the azonal ones, as response to their peculiar environmental conditions. Medium Hill shares the most species with other meso-LUs having in average $QS = 58.3\%$ ($SD = 11.6$). In fact, Medium Hill (MH) is rich in open, more or less scattered herbaceous habitats, inhabited by unspecialised assemblages of mobile species. In addition, MH borders on the most meso-LUs (eight), so that individuals migrate easily from one to the neighbouring

Table 3 Similarity (%) by qualitative (QS) (above the diagonal) and quantitative (PS) (below the diagonal) similarity indices for all combination-pairs of all meso-LUs

| Meso-LU | SCD | F | R | AF | TS | LH | MH | HH | M | H |
|---------|-----------|-------------|------|-------------|-------------|-------------|-------------|-------------|------|------|
| SCD | — | 50 | 48.1 | 38.5 | 32 | 60.4 | 38.2 | 38.4 | 35.5 | 38.6 |
| F | 44 | — | 48.1 | 34.6 | 28 | 60.4 | 47.1 | 35.6 | 25.8 | 35.1 |
| R | 40 | 47.1 | — | 60 | 44.1 | 64.8 | 65.1 | 61.5 | 47.5 | 53.3 |
| AF | 14.7 | 20.5 | 24.5 | — | 51.5 | 49.3 | 66.7 | 62.9 | 51.3 | 57.5 |
| TS | 16.4 | 15.9 | 24.6 | 37.9 | — | 41.8 | 53.7 | 52.9 | 50 | 56.3 |
| LH | 48 | 60.8 | 55 | 23.7 | 18.3 | — | 63.5 | 57.8 | 40.5 | 59.5 |
| MH | 43.6 | 47.7 | 43.9 | 44.7 | 28.9 | 57.5 | — | 76.2 | 51.1 | 60.7 |
| HH | 32.4 | 40.1 | 42.2 | 35.5 | 31 | 48 | 53.8 | — | 54.5 | 66 |
| M | 24.1 | 16.5 | 26.6 | 26.1 | 35.1 | 22.6 | 24.3 | 29.1 | — | 55.4 |
| H | 19.3 | 27.4 | 32.1 | 34.6 | 28.8 | 36 | 35.8 | 54.7 | 30.9 | — |

Highest similarity values recorded for each meso-LU are in bold

Table 4 Intrasimilarity, or average similarity, by quantitative index (PS_{av}) computed for all meso-LUs, taking into account all combination-pairs ($n = \dots$) between micro-LUs belonging to a given meso-LUs. When at least one or more combination-pairs are available, values and their standard deviations have been reported in brackets

| Meso-LU | PS_{av} |
|-----------------|-------------|
| SCD ($n = -$) | — |
| F ($n = 10$) | 31 (12.6) |
| R ($n = -$) | — |
| AF ($n = 1$) | 12.2 (—) |
| TS ($n = 1$) | 38.2 (—) |
| LH ($n = 10$) | 50.3 (7) |
| MH ($n = 66$) | 19.7 (13.1) |
| HH ($n = 28$) | 35.5 (15.1) |
| M ($n = 15$) | 29.1 (17.2) |
| H ($n = 1$) | 69.7 (—) |

unit. Very interestingly Highlands show higher QS values when compared with hilly meso-LUs than with the contiguous Mountain (Table 3). In this case, the higher presence of human-modified landscapes and the moderately continental climate with dryer and hotter summer within Highlands can explain this similarity pattern.

Looking at percentage similarity, Lower Hill and Fiumara show the most similar species assemblage (Table 3). During the summer some grassland species penetrate into Fiumara searching for refuges from the sun into small riparian oleander woods on the ‘fiumara’ bed. Moreover, Lower Hill and Fiumara are homogenised by summer aridity, both loosing any alimentary sources for adults. The least similar species assemblages inhabit Sandy Coastal Dunes (dry, soil nutrient poor, open formations) and Alluvial Fans (moist, soil nutrient rich, forest formations), because of their extremely different environmental conditions. Other considerations about PS affinities are the same made about QS . QS and PS show only one important difference. Higher similarity values are always attained by QS , demonstrating PS helpful in searching differences among species assemblages. In definitive, using PS it is possible to discriminate assemblages taking into account the functional role assumed by each species.

Intrasimilarity, or average similarity, by quantitative index (PS_{av}) was computed for all meso-LUs, taking into account all combination-pairs between micro-LUs belonging to each meso-LUs (Table 4). Intrasimilarity values could be considered as a measure of meso-LUs homogeneity. Among the meso-LUs having at least ten combination-pairs, and then statistically significant, the highest value of PS was registered within Lower Hill, because of strongly man-modified landscape marked by scarce wood remnants, and the lowest value within Medium Hill, because of moderately human modified status, showing more or less the same proportion of herbaceous and forest environments. A relatively high homogeneity has been found in High Hill, where human activities are poorly developed.

For a summary of many meso-LUs data, see Fig. 3.

Diversity at micro-scale

Species richness (S) of survey sites is strictly correlated with their Shannon diversity (H') ($r_p = 0.81$, $p < 0.0001$). A clear decrease of H' was recorded in four sample sites only (Table 5); TLe3 (*Quercus ilex* forest), TCe1 and TCe2 (*Quercus cerris* forests) are near to the climax stage, while RCol1 (*Medicago sativa* cultivation) is very far from the climax. Species favoured by larval (viz. *Satyrium ilicis* (Esper) within TLe3, *Thecla quercus*

Table 5 Data collected within Sila Greca's micro-LUs

| Name | N | S | H' | $1/\lambda$ | D1 | D3 | I_v | PS_{av} |
|-------|-----|----|------|-------------|---------|---------|-------|-------------|
| TLe4 | 12 | 3 | 1.04 | 1.78 | -4.4490 | 0.3667 | 0.96 | 4.1 (10.8) |
| TPi1 | 7 | 4 | 1.84 | 5.25 | -0.768 | -0.2000 | 0.48 | 16.5 (11) |
| TNo2 | 7 | 5 | 2.24 | 10.50 | 0.2948 | 0.6989 | 0.29 | 18.3 (11.6) |
| THe2 | 6 | 5 | 2.25 | 15.00 | 0.5654 | 0.7894 | 1.01 | 14.8 (12.5) |
| TNo3 | 5 | 5 | 2.32 | – | 0.3732 | 0.5124 | 0.17 | 25.1 (14.9) |
| SFag1 | 8 | 5 | 2.16 | 7.00 | -0.0890 | -1.3027 | 0.51 | 14.5 (9.5) |
| TLe1 | 11 | 6 | 2.48 | 9.17 | -0.0950 | 0.2974 | 0.78 | 16.3 (8.9) |
| TAf | 7 | 6 | 2.52 | 21.00 | -0.2840 | -1.1240 | 0.84 | 8.8 (11.8) |
| TLe5 | 16 | 7 | 2.41 | 5.46 | -0.6430 | 0.0551 | 0.34 | 20.5 (10.5) |
| TNo1 | 16 | 8 | 2.78 | 9.23 | 0.2279 | 0.3971 | 0.94 | 26.1 (13.3) |
| RLe1 | 19 | 9 | 2.90 | 9.00 | -0.0420 | 0.1998 | 0.92 | 11.4 (8.3) |
| TLe2 | 17 | 11 | 3.29 | 17.00 | -0.2320 | 0.0334 | 1.35 | 20 (8.3) |
| TLe3 | 53 | 11 | 1.98 | 2.36 | -3.5520 | 0.3625 | 1.00 | 16.9 (9.4) |
| TEu1 | 22 | 11 | 3.27 | 13.59 | 0.2834 | 0.4007 | 1.10 | 32.5 (16.2) |
| TAq | 21 | 11 | 3.01 | 8.08 | -0.3430 | -1.0367 | 0.97 | 13 (11.3) |
| TCi1 | 28 | 12 | 3.24 | 9.45 | 0.3978 | 0.5805 | 0.44 | 23.2 (12) |
| TQ1 | 38 | 12 | 3.17 | 8.90 | -0.0720 | 0.2808 | 1.71 | 23.4 (12.5) |
| THel | 35 | 13 | 3.55 | 14.88 | 0.4847 | 0.7145 | 0.81 | 26.8 (14.9) |
| TP1 | 72 | 14 | 3.36 | 10.14 | 0.4387 | 0.6511 | 0.77 | 29.1 (15.9) |
| RP2 | 37 | 14 | 3.31 | 8.88 | 0.3427 | 0.3446 | 0.97 | 17.5 (11.3) |
| TCe2 | 64 | 15 | 2.03 | 2.11 | -1.3670 | -0.1968 | 0.95 | 16 (11.4) |
| TPi2 | 27 | 15 | 3.66 | 17.55 | -0.1100 | -0.8322 | 1.11 | 21.1 (8.6) |
| TP2 | 52 | 16 | 3.39 | 8.29 | 0.2689 | 0.1692 | 0.73 | 32.7 (15.1) |
| SPi2 | 39 | 16 | 3.47 | 9.50 | 0.3947 | -1.5527 | 0.11 | 17.5 (10.6) |
| Tdun1 | 104 | 17 | 2.95 | 5.36 | 0.6195 | 0.4092 | -0.04 | 24.5 (12.7) |
| TCa1 | 54 | 18 | 3.57 | 10.30 | 0.0827 | -0.1907 | 1.00 | 27.2 (10.4) |
| TU11 | 94 | 19 | 3.13 | 5.42 | 0.3156 | 0.5093 | 0.23 | 28.1 (14.8) |
| TCa2 | 49 | 19 | 3.75 | 12.38 | -0.1330 | -0.2476 | 1.02 | 28.1 (11.6) |
| TLed | 59 | 19 | 3.85 | 14.14 | 0.1450 | 0.3946 | 1.04 | 28.9 (13.7) |
| RQ1 | 156 | 20 | 3.38 | 7.66 | -0.2360 | 0.3494 | 1.18 | 24.4 (10.5) |
| TCa | 61 | 20 | 3.87 | 14.76 | -0.1890 | -0.1500 | 1.25 | 27.3 (11.6) |
| TLS1 | 71 | 21 | 3.86 | 13.15 | 0.4344 | 0.5042 | 1.13 | 29.2 (16.7) |
| SPr1 | 45 | 22 | 4.18 | 23.02 | 0.3452 | -1.9836 | 0.77 | 18.2 (12) |
| RP1 | 68 | 24 | 4.03 | 14.15 | 0.3886 | 0.5298 | 0.97 | 23.2 (14.2) |
| TCe1 | 91 | 25 | 2.69 | 2.80 | -1.2670 | -0.2047 | 1.37 | 16 (12.2) |
| TAg | 116 | 26 | 3.57 | 7.19 | -0.2620 | -0.5530 | 1.26 | 19.3 (10.6) |
| TPr1 | 98 | 27 | 4.03 | 12.16 | 0.3125 | 0.3963 | 0.92 | 32.9 (16.8) |
| TAq1 | 94 | 29 | 4.47 | 22.19 | 0.0108 | -0.7583 | 1.33 | 20.4 (8.7) |
| RCo11 | 190 | 30 | 3.25 | 5.51 | 0.3024 | 0.3478 | -0.05 | 27.5 (13.9) |
| SRad1 | 95 | 30 | 4.24 | 15.95 | 0.4948 | -2.3277 | 0.79 | 17 (11.4) |
| Teuf1 | 157 | 31 | 4.17 | 12.07 | 0.2537 | 0.3821 | 1.01 | 30.6 (15.7) |
| TP3 | 57 | 31 | 4.56 | 26.16 | 0.2698 | 0.1102 | 1.10 | 28.7 (13.7) |
| TGin1 | 133 | 31 | 4.37 | 17.38 | 0.2912 | 0.0390 | 1.19 | 27.7 (13.4) |
| TTe | 111 | 36 | 4.09 | 10.18 | 0.3459 | 0.3443 | 0.45 | 28.7 (12.7) |

For each micro-LU are reported: number of individuals (N) and species (S) sampled; diversity indices values (Shannon's index, H' , and reciprocal form of Simpson's index, $1/\lambda$); D1 and D3 values in the Canonical Correspondence Analysis; community vulnerability Index (I_v); average similarity computed by quantitative index (PS_{av}) and its standard deviation, between parentheses, for all micro-LUs, taking into account all combination-pairs between them ($n = 43$). Micro-LUs are ordered by S increasing.

(Linnaeus) within TCe1 and TCe2) or adult feeding behaviour (*Polyommatus icarus* and *Colias crocea* (Geoffroy) within RCo11) dominate these species assemblages. Forests, whatever their origin, almost never show species richness values higher than meadows, pastures, or clearings (Table 5).

Azonal stands have seven unique species. Five of these are interesting from a faunistic viewpoint (*Pyrgus carthami*, *Gegenes nostradamus*, *Lycaeides abetonica*, *Polyommatus daphnis*, *Danaus chrysippus*). In addition, four species (*Pieris edusa*, *Anthocaris damone*, *Hyponephele lupina*, *Pararge aegeria*) achieve their maximum abundance in azonal biotopes, which act as dispersion centres. However, this observation should not be overemphasized. In fact, in summer high individual and species concentration occur along rivers and puddles, due to abundant and protracted flowering favoured by the prolonged presence of water. This fraction of the Sila Greca diversity is ecologically very fragile because of the small surfaces of suitable landscape units (Table 2).

Zonal stands have many more unique species (30) than azonal ones, thank to their great environmental heterogeneity along ecological successions, as well as to larger areas covered. Standard characteristics of these species are medium or low dispersal ability, habitat preferences for forest, and close feeding relations with near-to-climax vegetation (*Satyrium ilicis*, *Thecla quercus*, etc.). However, this group of species contains only three important species from a conservation viewpoint, i.e. *Melanargia arge*, included in the Annex II of the EC 92/43/EEC Habitat (1992), *Zerynthia polyxena*, included in the Annex IV of the same directive, and *Melitaea aetherie*, endangered at Italian national scale (Balletto and Cassulo 1995).

Micro-LUs species assemblages are more variable than meso-LUs, *PS* varying from 0%, to more than 65%. *PS* values equal to zero have been mostly registered for comparison-pairs including (1) near-to-climax micro-LUs belonging to different meso-LUs, or (2) near-to-climax and far-to-climax micro-LUs belonging to different meso-LUs, while the highest *PS* values have been often registered between near-to-climax or between far-to-climax micro-LUs belonging to the same meso-LUs. Among surveyed sites, the less similar in average at all are the azonal, near-to-climax and mountain micro-LUs, that show the best characterised species assemblages (Table 5).

Evaluation of community vulnerability

Results of the community vulnerability Index (I_v) have been reported in Table 5. We subdivided stands into four vulnerability categories, according to increasing I_v values: *no vulnerable* ($I_v \leq 0.39$), *low vulnerable* ($0.40 \leq I_v \leq 0.79$), *average vulnerable* ($0.80 \leq I_v \leq 1.19$) and *high vulnerable* ($I_v \geq 1.20$). The *No vulnerable* category includes mainly tilled lands, pastures and secondary formations, or micro-LUs having communities composed by very few individuals. The *Low vulnerable* category includes reforestation sites, meadows and pastures contiguous to near-to-climax formations, or stands embedded into a well-preserved environmental matrix. The *Average vulnerable* category includes the mature forests and clearings of various origin. The *High vulnerable* category includes only the mature forests and the clearings of a natural origin, as well as the “precious” talus slopes. This subdivision is probably arbitrary and results may be different for different landscapes. Results, however, remain useful for comparative evaluations within a given study area. A cartographic model of the distribution of community vulnerability was obtained by transposing results on a vegetation map (Bernardo et al. 1991) and grouping vegetation categories according to I_v values (Fig. 2b).

The greatest total vulnerability was recorded in the deciduous oak belt, where the assemblages were composed, more than in other areas, by species closely related to forest for food requirements and where human activities are limited by the rugged topography. The smallest vulnerability was recorded within the sclerophyll biome, where the assemblages were composed mainly by highly mobile taxa most with polyphagous caterpillars

and eurytopic adults. In other words, these assemblages show the consequences of human disturbance caused by increasing urbanisation and by intense ecosystem exploitation. At low altitude I_v values of the “fiumare” are relatively high. I_v values of Subatlantic *Fagus*-belt are low, probably because of the absence, in S. Italy, of species linked by feeding relations to the pine and beech forests. Human exploitation of the environment becomes the main factor influencing I_v values within hilly landscape units.

Discussion

Diversity analysis at micro-scale show that (1) few species dominate the species assemblage in some near-to-climax micro-LUs, and (2) human-modified micro-LUs often contain higher diversity than near-to-climax ones. At the light of these data, it is clear that diversity is inadequate to evaluate the conservation interest of a given micro-LUs, because the high availability of food sources for adult butterflies in herbaceous landscape units, and high mobility of meadow-living species lead to have this apparently contradictory diversity pattern. At this scale indeed the relation “high diversity–high conservation interest” sounds inadequate. The community vulnerability index (I_v) takes into account main life history traits of species (dispersal ability and niche choice) becoming very similar to a measure of “typicalness”, drawn from contextual evaluation of both diversity and auto-ecological data inherent in species composing butterfly assemblages. In Samways’ opinion (1994) “typicalness is probably more appropriate in the evaluation processes than is richness”. Maes and Van Dyck (2001) demonstrate that species having low dispersal abilities decrease in agricultural landscape, Bergman et al. (2004) that “more mobile species were significantly less demanding in regard to the amount of deciduous forest/semi-natural grassland”. The cartographic output obtained by the I_v mapping is in strong agreement with the conclusions of these authors. The cartographic model of landscape vulnerability of Sila Greca, with respect to human activities, based on I_v , is very similar to a “naturalness” map, because species assemblages show low vulnerability when located in perturbed environments. Very simple cartographic transposition and the simple conceptual comprehension of I_v make this index a useful tool for local decision-makers as concerns landscape planning and conservation goals.

Similarity analysis at micro- and meso-scale demonstrate the identity of meso-LUs from a species assemblage viewpoint and the functional value of this landscape unit, mainly at near-to-climax successional stages. Moreover, diversity values, sometimes contradictory at micro-scale, give good insight into naturalness at meso-scale. The low species richness values of Sandy Coastal Dunes and Fiumara meso-LUs (Fig. 3) are satisfactorily explained by their extreme environmental conditions for butterfly assemblages (low fresh water availability, and poor vegetal biomass), but human activities play also an important role, mainly in the impoverishment of vegetation cover. In fact, many towns and beach resorts are built along sandy coasts and near rivers. Moreover, water drainages are done for field watering, diminishing water disposal for vegetation. The impact of human activities is particularly evident in Low Hill meso-LU, being here the desertification process strongly favoured. In fact, hilly meso-LUs show a very low resilience, because of the low annual rain-falls and the low disposal of organic matter in the soil. Thus, man made environments, such as extensive cereal and citrus cultivations, are decisive in justify a 30% diversity loss within Low Hill in comparison to Medium Hill and High Hill meso LUs, where many natural patches are present (Fig. 3). The meso-LUs allows us to carry out conclusions only on the simple species number, because they represent functional landscape portions

individuated by using attributes objectively recognizable. As confirmed by similarity analysis, meso-LUs are very similar to true functional landscape unit. Probably, this is the nonarbitrary scale, invoked by Wiens (1989), at which biological function are clearly linked to seral processes that begin and end ‘inside’ (Brandmayr et al. 1998). Attempts towards the search of nonarbitrary scales in landscape studies, were previously done by other authors (Lapin and Barnes 1995: plants) (for a review see Mackey et al. 2001), but just little attention was devoted to dynamic trends inside the functional landscape unit, and towards the development of an evaluation protocol simple to apply for non specialists too.

While our micro-LU is easily identifiable with the biotope and the related diversity with the alpha-diversity (Cody 1975; Whittaker 1975), and our macro-LU is more or less identifiable with the regional scale and the related gamma- (Cody 1975) or epsilon-diversity (Whittaker 1977), some problems rise in the identification of our meso-LU. The most similar landscape unit is the ecotope, defined by Forman and Godron (1986) as “the smallest possible land unit, that is still a holistic unit”. Brandmayr et al. (1998) gave to the ecotope the following definition: “a basic landscape unit delimited mostly by its particular geomorphology, and guesting a certain number of more or less closely inter-related ecosystem (vegetation, faunal community) types, that built a well defined community complex”, emphasizing the importance of geomorphologic features and the dynamic relations among vegetation and animal seral communities. Brandmayr et al. (1998) proposed the eta-diversity (greek letter: η) as related biodiversity measurement. Eta-diversity and I_v values show a concordant distribution pattern in the Sila Greca territory (Fig. 2). Eta-diversity numbers have a very similar distribution of I_v values, we could imagine the former the ‘before’ and the latter the ‘after’ the beginning of landscape modifications by humans. I_v underlines the conditions in which ecotopes currently are, i.e. very fragmented, composed mostly by herbaceous formations (pastures, clearings and tilled-land of anthropic origin, often showing high species richness), surrounding forest isles (most with low species richness).

Conclusions

In this paper, butterfly assemblages were the tool, not the goal, of a research addressed to map areas vulnerable to human alterations. Usually, the faunistic component is the goal and landscape attributes the tool of a research. In our approach, the presence of endangered species for evaluating conservation interest of a given area is not strictly necessary. Indeed, taking into account the vulnerability of species assemblages by using the community vulnerability Index could be useful to prevent, or at least limit, local extinctions having broad implications for conservation planning.

Our bottom-up approach (micro-to-macro) for linking biodiversity of different landscape scales seems to be useful in conservation strategies, because very simple to apply over thousands of hectares, providing at the same time an effective framework for comparing and assessing the diversity of species assemblages within different landscape units. In particular, the cartographic transposition of eta-diversity is very easy to practice and it fits to a meso-scale landscape unit, here identified with the ecotope, that has more or less homogeneous zoological potentialities. In other words, at this scale patterns and processes seems to be strictly linked as proposed by Hobbs (1997), proving that this approach to landscape ecology is useful for conservation science. Anyway, studies on further animal groups are needed to give more support to the model of alpha-, eta- and gamma-diversity proposed here.

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Habitat use of booted eagles (*Hieraetus pennatus*) in a Special Protection Area: implications for conservation

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Abstract We examined the patterns of habitat use of six radio-tagged booted eagles (*Hieraetus pennatus*) in a Special Protection Area (SPA) in southeastern Spain. Variable percentages of radio locations (20.8–72.0 %) and home range areas (45.2–81.3 %) lay outside the SPA limits. A model selection procedure showed that habitat use was mainly influenced by habitat type and the distance to the nest. Edges and open lands were the most selected habitat types at long distances, while the probability of forest use strongly decreased with the distance. We conclude that effective conservation strategies for this species should encourage not only the protection of the forest nesting habitats, but also the traditional agricultural practices of the surrounding agroecosystems.

Keywords Birds Directive · Habitat selection · *Hieraetus pennatus* · Home range · SPA · Traditional agroecosystems

Introduction

The Council Directives 79/409/EEC on the conservation of wild birds (Birds Directive), and 92/43/EEC on the conservation of natural habitats and of wild fauna and flora (Habitats Directive), have led to the establishment of the Natura 2000 Network, a system of protected areas in the European Union. This network includes Special Protection Areas for birds (SPAs) and Special Areas of Conservation (SACs), which are designated by the Member States in order to guarantee the favourable conservation status of species and habitats of Community interest (Ostermann 1998). The evaluation of the Natura 2000 Network as a tool for nature and biodiversity conservation is receiving increasing attention in scientific papers (Bouchet et al. 1999; Thompson et al. 2001; Lund 2002; Dimitrakopoulos et al. 2004;

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Jackson et al. 2004). and the importance of maintaining traditional agricultural practices for the management of many of the designated sites and for the conservation of the target species that inhabit them has been especially recognized (Beaufoy 1998; Ostermann 1998; Muller 2002). Surprisingly, although the Birds Directive was adopted 13 years before the Habitats Directive, SPAs have received much less attention than SACs in scientific literature; thus, much more research must be conducted to evaluate the effectiveness of those sites designated for the protection of bird species. Nonetheless, some authors have pointed to the importance of the Habitats Directive for the conservation of many bird species in Mediterranean landscapes (Beaufoy 1998), where the mosaic of woodlands, scrubs, pastures, and unirrigated crops provide a diversity of habitats for wildlife (Blondel and Aronson 1999).

Birds of prey are among those species for which the efficacy of conservation strategies should be monitored and evaluated regularly; they usually have large territories or home ranges and a large capability of movement, while most species use more than one type of habitat to satisfy their ecological requirements (Newton 1979). These characteristics make raptors ideal species for testing the performance of a protected area in maintaining a favourable biodiversity conservation status (Sergio et al. 2005). In this paper, we examine the habitat use of breeding booted eagles (*Hieraetus pennatus*) in an SPA designated for this species and located in the region of Murcia (southeastern Spain). The booted eagle is a medium-sized raptor species and a trans-Saharan migrant, which usually nests in trees and, more rarely, on cliffs (del Hoyo et al. 1994). Although it is a common species of the forests and woodland areas of the Iberian Peninsula, several authors have shown that booted eagles select areas with a mixture of woodlands and open lands, suggesting the importance of extensive crops adjacent to the nesting woodland patches as foraging habitats for the species (Sánchez-Zapata and Calvo 1999; Suárez et al. 2000). Our objective was to confirm this importance by analysing habitat use of radio-tagged individuals in the study area, and assessing the contribution of the different habitat types to the foraging activities of booted eagles.

Methods

The study was conducted between 1999 and 2004 in the ‘Sierras de Burete, Lavia y Cambrón’, a Special Protection Area (ES0000265) of 21482 ha located in southeastern Spain (38°00' N, 1°45' W). Elevation ranges from 550 to 1521 masl and the climate is Mediterranean, with a mean annual rainfall of 400 mm. The landscape is characterized by mountain slopes covered by pine forests (*Pinus halepensis*) interspersed with traditional agroecosystems (cereals, vineyards, olive and almond groves). The study area was designated SPA by the Autonomous Community of Murcia in 2001, but its limits encompass only the forested core area of the massif, and most adjacent crop areas lie outside. It has one of the highest densities of booted eagles and short-toed eagles *Circaetus gallicus* in Europe (Martínez 2002), and meets the SPA criteria for both species. During the study period the booted eagle population in the SPA was estimated at 25–30 breeding pairs (Martínez et al. in press).

Between 1999 and 2003 we trapped four adult female and two adult male eagles during the early brood rearing period (when the young were about 10-days old),

using a dho-gaza net placed near the nest using a live eagle owl (*Bubo bubo*) as a lure (Bloom et al. 1992). The selection of nesting territories for trapping was constrained by successful reproduction and available open space to place the nets near the nest. Each trapped bird was fitted with a 13 g radio transmitter (AYAMA, Barcelona) attached as a backpack harness made from Teflon ribbon (Kenward 2001), and tracked for a 10 h period every 6–7 days, until they left the study area in late September. Three of the females returned to the study area the next year, and thus were tracked in two different years. In all cases, the young of the trapped individuals were successfully raised.

Radio locations were made by visual observation with the aid of a portable receiver (AYAMA model TSN-1) with a tree-element yagi-antenna, and an off-road vehicle. Locations were plotted in the field on 1:25,000 scale topographic maps with the help of aerial photographs and a GPS unit. For the analysis of habitat use, we only considered locations recorded at a minimum of 30-min intervals (Lair 1987), and where foraging behaviour was observed (gliding and hunting). We considered three habitat types: woodland, open land (scrubland, arable field) and edges between them. A radio location was assigned to the edge type when the bird was observed within a 20 m buffer strip around a border between two other habitat types.

Home range sizes were determined using the 95% fixed kernel estimator. Habitat selection was analysed within the home range using a modification of the method for central-place foraging animals proposed by Rosenberg and McKelvey (1999). For each radio-tagged eagle, we used its estimated home range as the available habitat. Within each home range, a number points equating the number of radio locations were randomly located. The result matrix was analysed with Generalized Linear Mixed Models, considering individuals as a random factor and habitat type, distance to the nest and sex as fixed factors (Carrete and Donázar 2005). Models were performed using a logit link function and binomial errors, and compared with the bias-corrected version of Akaike's Information Criterion (AICc):

$$\text{AICc} = -2(\log \Lambda) + 2K + \frac{2(K+1)}{n-K-1}$$

where $\log \Lambda$ is the log-likelihood function, K is the number of parameters estimated and n is the sample size. Models were ranked using AICc differences (Δ_i) and Akaike weights (w_i). Δ_i were calculated as the difference between the AICc of each model and the AICc of the best model. Models with $\Delta_i < 2$ can be considered alternative models to the selected model (Burnham and Anderson 2002). Akaike weights may be interpreted as the probability that model i is the actual best model of the set, and were computed as:

$$w_i = \frac{e^{-\frac{\Delta \text{AICc}_i}{2}}}{\sum e^{-\frac{\Delta \text{AICc}_i}{2}}}$$

All statistical analyses were performed with the *R* statistical package (R Development Core Team 2005).

Results

The total number of radio locations was 279, and home range sizes ranged from 8839 to 23334 ha (Table 1). Variable percentages of radio locations (20.8–72.0 %) and home range areas (45.2–81.3 %) lay outside the SPA limits (Table 1, Fig. 1). The model selection procedure (Table 2) showed the importance of the three variables

Table 1 Radio locations and home range sizes (95% fixed kernel estimator) of six Booted Eagles in the Special Protection Area of the ‘Sierras de Burete, Lavia y Cambrón’ and its surroundings (region of Murcia, SE Spain)

| | Radio locations | | | Home ranges | | | |
|-------------------|-----------------|-----------|-----|-------------|-----------|----------|-----------|
| | % inside | % outside | n | Fixes | Size (ha) | % inside | % outside |
| Female #1 | 79.2 | 20.8 | 53 | 90 | 16710 | 54.8 | 45.2 |
| Female #2 | 58.9 | 41.1 | 56 | 92 | 10108 | 50.6 | 49.4 |
| Female #3 | 60.0 | 40.0 | 35 | 43 | 8839 | 43.2 | 56.8 |
| Female #4 | 46.0 | 54.0 | 63 | 75 | 11263 | 36.2 | 63.8 |
| Total females | 60.4 | 39.6 | 207 | — | — | — | — |
| Male #1 | 40.9 | 59.1 | 22 | 28 | 17374 | 25.2 | 74.8 |
| Male #2 | 28.0 | 72.0 | 50 | 80 | 23334 | 18.7 | 81.3 |
| Total males | 31.9 | 68.1 | 72 | — | — | — | — |
| Total individuals | 53.0 | 47.0 | 279 | — | — | — | — |

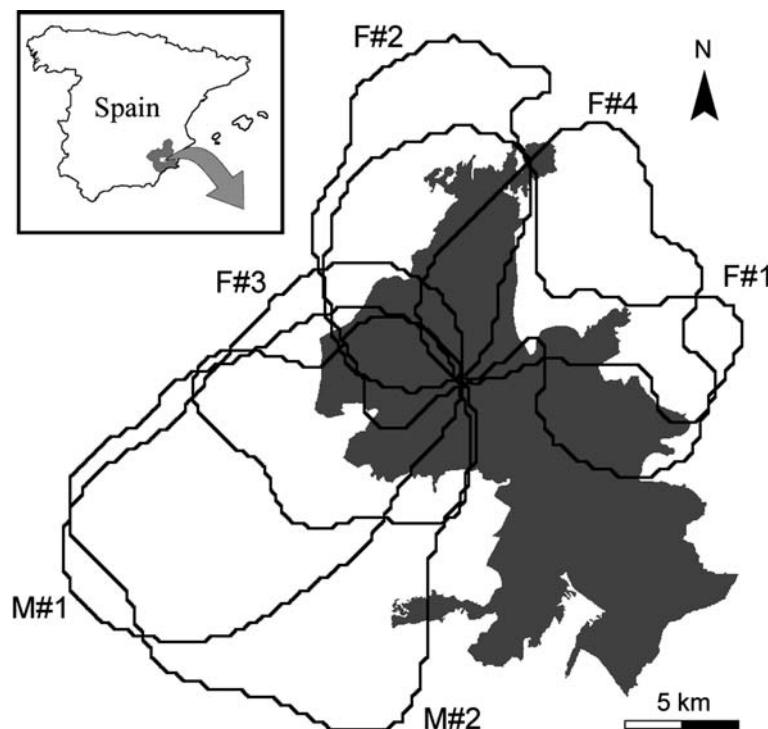


Fig. 1 Home ranges (95% fixed kernel estimator) of the six radio-tagged Booted Eagles in southeastern Spain (F: females; M: males). The shadow area corresponds to the Special Protection Area

considered in explaining the probability of habitat use. The best model was a complex model ($K=13$) which included distance to the nest, habitat type and sex, together with their interaction terms. However, the alternative, second best model ($\Delta_i < 2$) did not incorporate sex, thus incorporating a lesser number of parameters ($K=7$). For simplicity reasons, we show in Fig. 2 the representation of the fitted values of this alternative model, revealing the different patterns of habitat use in relation to distance. As distance increases, the probabilities of edge and forest use decrease, but remains approximately constant for open land. Consequently edges and open lands tended to be more frequently used at large distances. The variance component attributed to random effects in the best model was very low (0.0058), indicating negligible differences among individuals.

Discussion

Although most of the foraging radio locations were obtained inside the SPA, especially in the case of the females, our findings show that the booted eagles used a substantial proportion of non-protected territory within their home ranges. Moreover, although most of the radio locations were obtained in forests, edges were undoubtedly the most selected habitat type, even at short distances from the nest. The probability of forest use strongly decreases with the distance, while the probability of open land use remains approximately constant over the entire range of distances.

The booted eagle is a dietary generalist, and prey from open areas (pigeons, partridges, rabbits and lizards) form an important part of its diet (Martín and López 1996; Martínez and Calvo 2005). In Doñana National Park (SW Spain), the species shows a preference for wooded zones with nearby crops and open areas (Suárez et al. 2000). On a countryside scale, the extension of dryland crops and the length of edges are good descriptors of booted eagle abundance (Sánchez-Zapata and Calvo 1999). The results of these authors coincide with ours obtained on a home range and individual habitat use scale.

Booted eagle females, as many birds of prey, spend a lot of their time near their nests, only contributing to the feeding of their chicks to any great extent when they

Table 2 Results of the model selection procedure for habitat use analysis

| Model | K | AICc | Δ_i | w_i |
|--------------------------|-----|--------|------------|-------|
| Distance * Habitat * Sex | 13 | 651.35 | 0.00 | 0.538 |
| Distance * Habitat | 7 | 651.65 | 0.31 | 0.462 |
| Distance + Habitat + Sex | 6 | 686.07 | 34.72 | 0.000 |
| Distance + Habitat | 5 | 691.36 | 40.01 | 0.000 |
| Distance * Sex | 5 | 723.12 | 71.77 | 0.000 |
| Distance + Sex | 4 | 726.71 | 75.36 | 0.000 |
| Distance | 3 | 731.67 | 80.33 | 0.000 |
| Habitat * Sex | 7 | 732.28 | 80.93 | 0.000 |
| Habitat | 4 | 738.87 | 87.52 | 0.000 |
| Habitat + Sex | 5 | 740.73 | 89.38 | 0.000 |
| Sex | 3 | 779.60 | 128.25 | 0.000 |

Models are ranked according to AICc values and Akaike weights (w_i). Asterisks indicate a model structure with interactions among variables. K : number of parameters in the model

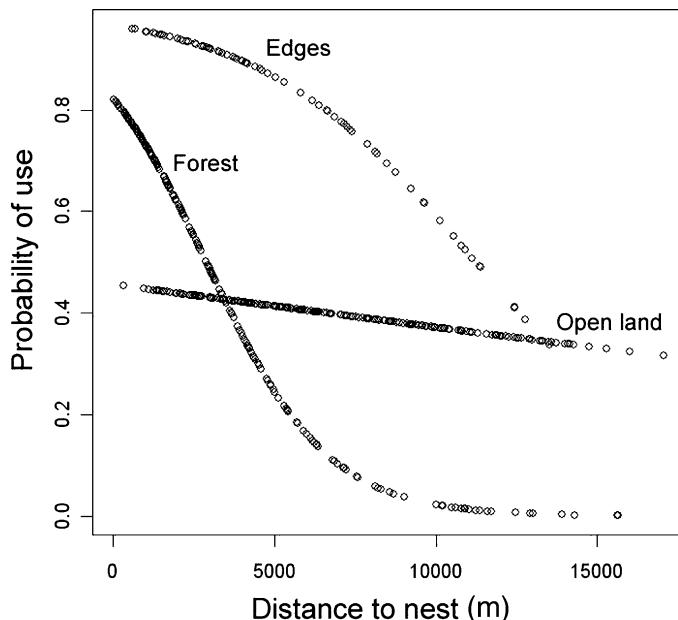


Fig. 2 Estimated probabilities of habitat use by Booted eagles, as a function of distance and habitat type

have reached a certain age (Newton 1979; Hubbert et al. 1995). This behaviour can influence the pattern of habitat use and explain the inclusion of sex in the best model of our selection procedure. However, the second best, alternative model did not include sex, which suggests that sex-related differences may be of minor importance in relation to the other two explaining variables.

As in the case of other tree-nesting raptors, the conservation of the booted eagle does not only depend on protecting forest areas, but also implies the protection of wide buffer zones of traditional farming practices and crops (Bakaloudis et al. 1998; Sergio and Bogliani 199; Suárez et al. 2000), and the development of management and conservation policies that should bear in mind the importance of such ecosystems (Bignal and McCracken 1996). In the last few decades, traditional Mediterranean agricultural systems have been damaged by human intervention in the form of intensive irrigation (Fernández-Alés et al. 1992; Martínez-Fernández et al. 2000). Furthermore, the European agricultural policy (CAP) has encouraged changes in the crops grown, the mechanisation of agricultural practices, the disappearance of hedges and the increased use of agrochemicals (Ruiz Pérez 1990). The result has been a substantial change in the agricultural landscape and extremely negative effects on biodiversity (Tella et al. 1998). However, the adoption of agro-environmental improvement programmes (e.g. the European Community Regulation 2078/92) may help to favour the maintenance of landscape heterogeneity and the conservation of dryland crops, field margins and ecotones, on which the populations of the main prey species so closely depend (Lombardi et al. 2003).

We concluded that although the Special Protection Area may have a positive effect on maintaining favourable conditions for the nesting success of the booted eagle population in the study area, such success also depends on the adjacent

agricultural fields and scrublands for hunting activities. An effective conservation strategy for this and other Mediterranean forest raptor species should encourage the development of environmentally-friendly agricultural policies and, ideally, the design of a system of protected areas based on a broad scope of criteria, in which traditional agroecosystems are included.

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Is the wild rabbit (*Oryctolagus cuniculus*) a threatened species in Spain? Sociological constraints in the conservation of species

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Abstract The Wild rabbit (*Oryctolagus cuniculus*) is an endemic species of the Iberian Peninsula and is essential for the conservation of endangered predators. Rabbits are also of high importance as a hunting species. From 1988, rabbits suffered the severe effects of rabbit hemorrhagic disease, which caused large declines in most populations. Despite this fact, the National Red Data Lists continued to classify rabbits as a “Least Concern” species. We used available hunting bag data from 1973 to 2002 to model national trends of rabbit abundance and to evaluate the conservation status according to the criteria of the National Red Data List and the World Conservation Union (IUCN). Generalized Additive Models were used as the statistical framework. The rabbit population of Spain suffered a large decline of about 71% between 1973 and 1993. This decline was 49% in the period 1980–1990. Based on both Spanish and World Conservation Union criteria, rabbits should be listed as ‘Vulnerable’, which demands a Conservation Plan Program. We suggest that the lack of concordance between the best available evidence and the conservation status of the species is a consequence of sociological constraints in conservation decisions. Rabbit conservation could face strong opposition from important socio-economic lobby groups (hunters and farmers). As such, governments and researchers may prefer to exclude rabbits from any status category requiring conservation action, despite the evidence of decline. We call for the urgent development of a nation-wide conservation program for rabbits which includes both socioeconomic constraints and the available biological data on population trends.

Keywords Decline · GAM · Haemorrhagic disease · Hunters · Population trends · Rabbit · Spain · Threatened species

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Introduction

The Wild Rabbit (*Oryctolagus cuniculus*) is an endemic species of the Iberian Peninsula (Thompson and King 1989; Monnerot et al. 1994), although it has expanded in range in Europe and has been introduced to many other parts of the world. The species is now considered a pest in many places and most management strategies have been directed towards population control (Drollette 1996). In its native range including Spain, however, the rabbit may be considered a key element of the ecosystem, and therefore of high conservation value. In fact, rabbits represent the bulk of the diet of many Iberian predators (Delibes and Hiraldo 1981), and are the key prey species of several critically endangered species, including the Iberian lynx (*Lynx pardinus*) and Iberian Imperial Eagle (*Aquila adalberti*) (Ferrer and Negro 2004).

Added to their functional importance in Spanish ecosystems, rabbits often arouse polarized social and economic interests. On the one hand, rabbits are traditionally one of the most important game species in Spain (REGHAB 2002) and therefore hunters have an interest in keeping their numbers high. On the other hand, the species causes significant agricultural damage and so farmers call for rabbit populations to be controlled or eradicated.

Although rabbits are historically numerous and widespread on the Iberian Peninsula, the introduction of myxomatosis into the wild in the 1950s caused a significant drop in their population (Muñoz 1960; Thompson and King 1989). In the following years rabbits attained some natural immunity to the disease, but in 1989 a new viral epizootic, rabbit hemorrhagic disease (RHD), reached Spain and rabbits suffered mortality close to 80% in most populations (Peiró and Seva 1991; Blanco and Villafuerte 1993; Villafuerte et al. 1995; Calvete et al. 2002). From the first appearance of RHD to 1993, the decline in the rabbit population was estimated to be around 55% based on a questionnaire survey answered by hunters (Blanco and Villafuerte 1993). Despite such evidence, the National Red Data List based on the Red Data Book listed the rabbit as a “Least Concern” species (Blanco and González 1992).

It now appears that the newest edition of the National Red Data List (currently in preparation) will again list the rabbit within the “Least Concern” category. At present the only available population decline estimate on a national scale comes from the survey conducted by Blanco and Villafuerte (1993), and updated information based on a rigorous monitoring program of rabbit populations is lacking.

Monitoring abundance trends of wildlife populations is an essential component of any management program (Geissler and Sauer 1990; Thomas and Martin 1996; Fewster et al. 2000), and should be used to evaluate the current status of the species for its potential inclusion on national or international red lists of endangered species. The lack of nation-wide survey schemes for common species is a problem in many wildlife monitoring programs (Barker and Sauer 1992; Thomas and Martin 1996).

National monitoring programs are usually based on indirect measures of abundance such as count estimates along fixed routes (Droege and Sauer 1990; Fewster et al. 2000). However, game species show an additional advantage because hunting bag data can be used as a proxy of abundance across time (e.g. Potts et al. 1984; Baines and Hudson 1995; Cattadori and Hudson 1999; Kitson 2004). The best-known example comes from fisheries, where management is primarily based on catch data (Hilborn and Walters 1992). One major concern, however, is that harvest records do

not reflect true variations in species abundance (Gilpin 1973), although some studies indicate that correlations may be good (Royama 1992; Cattadori et al. 2003; Kitson 2004). Hunting statistics in Spain are available from 1973, and these may be the best data available for the determination of temporal dynamics and trends of game species across the country. Unfortunately, they have been misused by managers and researchers in Spain.

In addition to the lack of efficient survey methods and adequate data for the analysis of population trends, several problems are related to the selection of the analytical procedures to determine the magnitude and the direction of the trend, two essential pieces of data from the perspective of monitoring. As a consequence, a diverse and complex range of methods has been employed (reviewed in Thomas and Martin 1996; Fewster et al. 2000). The recent use of generalized additive models (GAMs) has shown flexibility and robustness when analyzing abundance trends of bird species over different source data and other monitoring features (Fewster et al. 2000).

In this paper, we describe for the first time the population trends of rabbits in Spain during the period 1973–2002. We used available hunting records as the source of abundance data across years and GAMs as the statistical framework to analyze trends. This information was used to identify the true conservation status of wild rabbit populations in Spain according to IUCN Red List categories guidelines and principles (IUCN 2001). We also discuss the sociological context of rabbit conservation in Spain and its potential solutions.

Methods

Hunting statistics

We obtained hunting bag data from the Ministry of Agriculture and Fisheries of Spain. This information is free and at the time of this study was available from 1973 to 2002. Data are based on questionnaires that all owners of hunting lands are required to complete each year. Ministry of Agriculture obtained a summary value of the bag record in each province by summing the data from each hunting land in each province for each year. The number of rabbits hunted is recorded for all Spanish provinces ($n = 50$). Provinces that had records for less than 20% of years were excluded from the study. We did not include hunting records from the Balearic or Canary islands because our aim was to check population trends in the area where rabbits are endemic and not in those areas where it may be considered an invasive species (Thompson and King 1989). Our final data set was drawn from 45 provinces from across the country. We used a relatively long time series for the analysis, starting in 1973, approximately 20 years after the first myxomatosis outbreak (Muñoz 1960). The time series ended in 2002, 14 years after the first detection of RHD in Spain (Argüello et al. 1988). Because we used bag records for each year in the series as the data points in the analyses, our study was based on data for 30 years.

Hunting statistics may be considered a good description of rabbit populations in each province because hunting lands cover 70–75% of Spain, with similar figures in all provinces (REGHAB 2002). Because the number of rabbits hunted may be partially due to hunting effort, this factor needs to be controlled in the analysis of

population numbers (Bostford et al. 1983; Cattadori et al. 2003) by using the number of hunting licenses issued as a measure of hunting effort in each province and in each year.

In all provinces and across the study period, rabbit hunting was regulated based on annual quotas proposed by hunters each year on the basis of the hunting bag of the preceding year. We thus considered that hunted rabbits were a suitable proxy of rabbit abundance in the hunting lands of Spain. In some cases, hunters imposed limitations in the form of restricted quotas, but these limitations were not related to rabbit abundance (Angulo and Villafuerte 2003). This is important because harvesting theory predicts that when density is low hunters tend to reduce quotas, which can lead to underestimations of population size. In contrast, when density is high hunters tend to increase quotas and so true numbers could be overestimated (Gilpin 1973; Cattadori et al. 2003). Both factors could influence trend estimates, but the lack of correlation between rabbit abundance and restricted quotas in Spain may minimize this source of bias.

Analyzing population trends by fitting generalized additive models (GAMs)

Most analyses of population trends have been conducted using route regression, Poisson regression or Mountford methods (e.g., Geissler and Sauer 1990). However, these methods cannot be used to extract genuine changes or trends from noisy data and they are ill suited to the investigation of nonlinear population trends (Siriwardena et al. 1998; Fewster et al. 2000). These problems can be overcome by using smoothing algorithms applied to abundance estimates (Fewster et al. 2000). Several of these smoothing techniques have been applied to bird census data both in North America and the United Kingdom (James et al. 1996; Siriwardena et al. 1998). GAMs extended these procedures, allowing both the incorporation of smoothing algorithms and a comprehensive modeling framework (Fewster et al. 2000). GAMs are an extension of generalized linear models (see Hastie and Tibshirani 1990) that allow any shape in the curve of the abundance estimates, through a range of non-parametric models (Fewster et al. 2000), and are thus a very flexible way to model how a response variable (e.g., population abundance) changes in response to several predictors (e.g., year and site). In a GAM, the level of smoothing (i.e., roughness) of the curves is defined in the model by the degrees of freedom (Hastie and Tibshirani 1990; Fewster et al. 2000). Our model took the following form:

$$\text{abundance index} = \text{site effect} + \text{smooth (year)}$$

For a comprehensive explanation of the procedures used to calculate the abundance index of the counts and the methods of GAM fitting, see Fewster et al. (2000). The site predictor may be of little biological interest but it has been incorporated into the model because abundance is likely to differ between sites. In our study the main predictor is year, which is represented as a smooth curve with predetermined degrees of freedom. We fitted curves based on splines (Hastie and Tibshirani 1990; Fewster et al. 2000), which were chosen to satisfy a penalized least square criterion, optimizing fit but penalizing roughness (Fewster et al. 2000). We used the recommendations of Fewster et al. (2000) and in our modeling framework we set the degrees of freedom to be 0.3 times the number of years in the time series, in our case 10.

In contrast to count data used in other monitoring programs (e.g., Geissler and Sauer 1990; Fewster et al. 2000), our model was based on a response variable in the form of an index (bag record/hunting effort). The data were log-transformed and then fitted to a GAM with Gaussian errors and identity link (Hastie and Tibshirani 1990). To evaluate whether population changes observed in the data were statistically significant, we calculated confidence intervals for abundance index estimates from the GAM curves by bootstrapping (Fewster et al. 2000). We performed 399 replicates with replacement of the data for each year and fitted a GAM curve for each replicate, thus obtaining a series of abundance index replicates which were used to obtain 95% confidence intervals following the methods of Buckland (1984) and Fewster et al. (2000).

Goodness of fit testing of our model was performed using plots of residuals and standard errors. We used the partial deviance residuals which measured the difference between the log-likelihood of the fitted model and the saturated model (Hastie and Tibshirani 1990). We considered a model as satisfactory when the residuals were distributed evenly above and below the fitted curve and the standard errors were small (Fewster et al. 2000).

We also calculated significant turning points in the time series using the methods of Siriwardena et al. (1998) and Fewster et al. (2000). We computed second derivatives (rates of change of the rates of change) of our abundance index estimates and their 95% confidence intervals from the 399 bootstrapped replicates. We calculated second derivatives from the 6th differences in equation 11 from Fewster et al. (2000). We also used a value of $r = 1$ (window size) in Equations 9, 10 and 11 from Fewster et al. (2000). Those years that did not contain a zero may be considered as years with a significant curvature in the trend. These turning points are an objective measure of significant decline or increase years and they may also be used to divide the time series into parts with similar trends (Siriwardena et al. 1998; Fewster et al. 2000). Because these turning points are associated with changes in the rate of change (e.g. changes in population growth) rather absolute values of abundance index, it is possible to detect significant decline although absolute values of abundance index did not reflect a clear population reduction.

For all analyses we used S-Plus code from Dr. R. Fewster with some modifications to accommodate Gaussian errors instead of Poisson errors. Analyses were run in S-Plus 2000 for Windows (Mathsoft Inc. 1999).

Assignment of a threatened category

In Spain, the conservation of species is based on the criteria established in the national list of threatened species (hereafter CNEADI, the Spanish acronym). This list only recognizes two threatened categories: Endangered (EN) and Vulnerable (VU). We used our data to evaluate rabbit status according to the criteria of the CNEADI.

We also evaluated rabbit status for the three threatened categories established by the IUCN: Critically Endangered (CR), Endangered (EN) and Vulnerable (VU) (IUCN 2001). Each level of threat (CR, EN or VU) is defined by a range of quantitative criteria, and a taxon that meets any one of the criteria for a threat level is assigned to that level.

Results

After controlling for the number of hunting licenses, the number of rabbits hunted ranged between 0 and 97.68 (mean \pm SE: 5.13 ± 0.23 considering data from all provinces and years). The highest number of rabbits hunted (averaged over all years) was found in Toledo, a province of central Spain (mean \pm SE: 23.81 ± 4.09) and the second highest was found in Cádiz, in southern Spain (mean \pm SE: 22.26 ± 1.43) (Fig. 1). The two lowest mean abundances were found in two northern provinces: Vizcaya (mean \pm SE: 0.0020 ± 0.0009) and Guipúzcoa (mean \pm SE: 0.017 ± 0.003). Figure 1 shows the pattern of rabbit abundance in Spain over the entire 30-year period considered. Overall, the highest number of rabbits hunted were found in central and southern Spain (Fig. 1).

Figure 2 shows the GAM trends for the abundance index with six different degrees of freedom: 3, 6, 10, 12, 16 and 20. Visual inspection of the five curves reveals that our ‘*a priori*’ selected condition of 10 degrees of freedom was indeed the best choice. The curve generated using 10 degrees of freedom revealed new features of the trends compared to 3 and 6 degrees of freedom, without being too rough. Values above 10 degrees of freedom generated rougher patterns, and as a consequence they lacked the smooth features that help to characterize true trends.

Diagnostic plots (Fig. 3) showed good fits of all GAMs with well distributed residuals around the index curve and very narrow confidence intervals. For brevity, here we only show the partial deviance residuals for the overall data.

Considering all regions together, rabbit populations in Spain suffered a major decline of about 71% when the years with the highest and lowest abundance indexes were compared (1973 vs. 1993) (Fig. 4). The series shows three significant negative turning points detected by the values of second derivatives of abundance index



Fig. 1 Map of rabbit abundance in Spain based on the distribution of mean values of hunting bags (controlled by the number of licenses issued) from 1973 to 2002. Colored areas represent different values according to quartile distribution. Black and white areas represent the highest and lowest values, respectively (first and last quartiles of the distribution), while grey areas represent medium values of abundance (higher according to intensity)

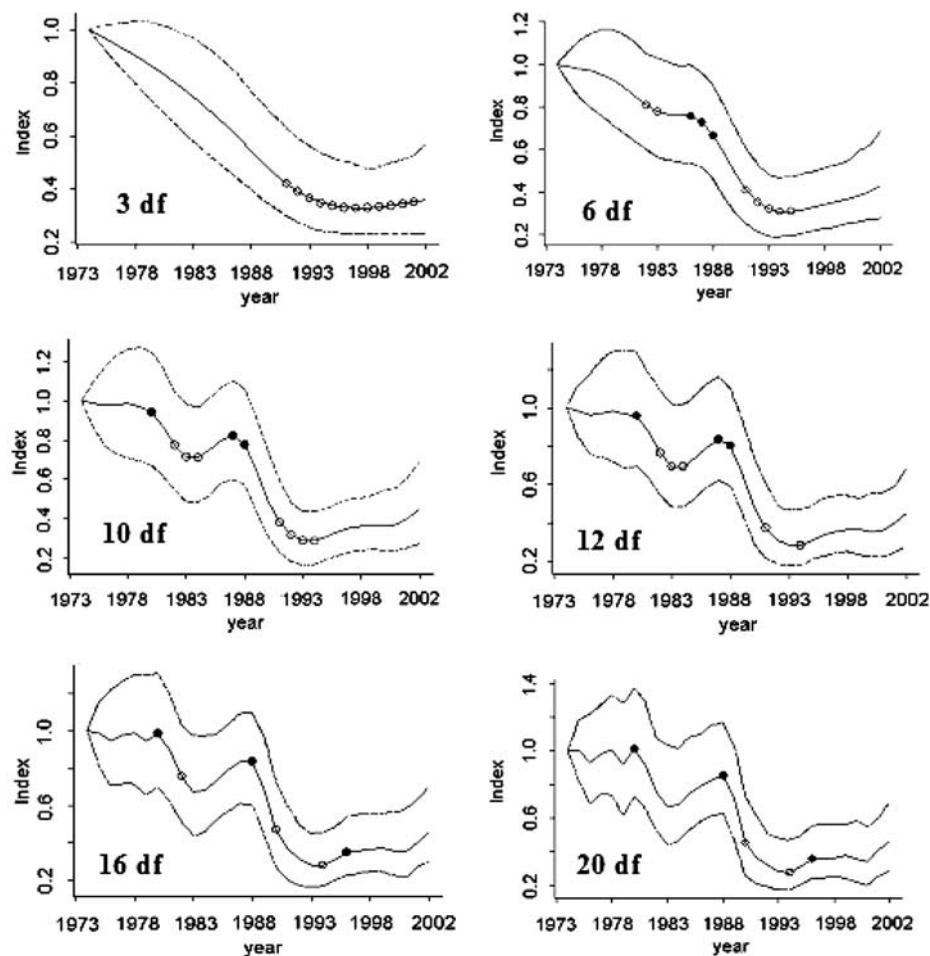


Fig. 2 Abundance index GAMs with different degrees of freedom fitted to hunting bag records from 1973 to 2002 in Spain

(Fig. 4, Table 1); the first was in 1979–1980, when a 13% decline between years was observed, but was followed by a significant positive turning point in 1982. During the period 1982–1987, and previous to the second significant negative downturn, rabbit populations increased. During 1987–1989 rabbit populations suffered a second crash, reaching minimum levels in 1993. The decrease between 1987 and 1993 totaled 48%, a very significant reduction in only 6 years, and a similar decrease was observed for several 10-year periods of the series. For example, a 49% decline was observed during the period 1980–1990 (a 10 year period very close to the publication of first Red Data Book in Spain). It is interesting to note that although a significant downturn was observed in 1987–1988 (a 13% decline from the previous year), the largest decline for any two years when absolute values of the abundance index were inspected was observed between 1988–1989, with a 15.5% reduction.

From 1993 to 2002 rabbit populations showed a slow but continuous recovery, although in 2002 abundance was still 55% lower than in 1973. Although the major

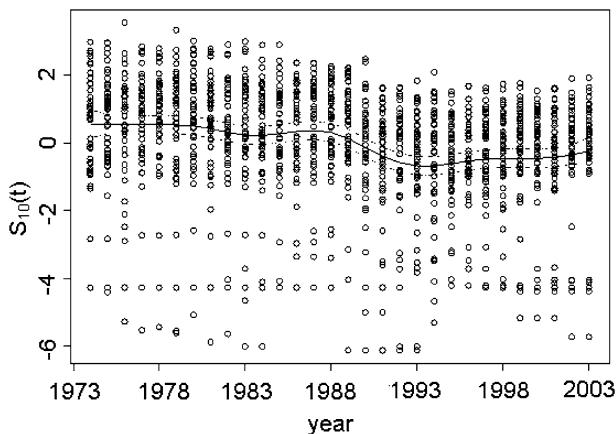


Fig. 3 Residual partial plot for the year effect curve $S_{10}(t)$ from a GAM with 10 degrees of freedom fitted to hunting bag records controlled by the number of licenses issued. Shown are 2 SE bands (dashed line), partial deviance residuals (black dots) and a rug plot. The figure shows the balanced distribution of the residuals around the index curve and very narrow confidence intervals

declines were mainly observed in the late 1980s, we noted that the decline was constant from 1973, with a 22.2% decline observed up to 1987.

We next fitted different GAMs to different regions with the aim of testing the generality of the decline pattern. We selected four regions: Galicia (NW Spain), Castilla-La Mancha and Madrid (Central Spain), Valencia and Murcia (E Spain) and Andalucía (S Spain). The populations of north-west Spain suffered declines similar to those observed in the overall pattern, although less pronounced, and we also observed a pronounced decline in the last 5 years (Fig. 5a). In these populations, the relatively large confidence intervals probably explain the non-significant nature of the downturns observed in the years 1979, 1987 and 1997, when detected declines for

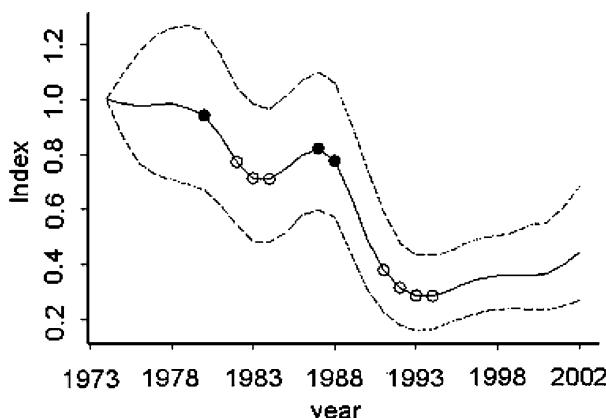


Fig. 4 Index curve showing rabbit population trends in Spain during the period 1973–2002. The solid line shows the abundance index from a GAM with 10 degrees of freedom. Dashed lines represent upper and lower 95% bootstrapped confidence intervals. Full circles correspond to significant negative turning points and empty circles represent significant positive turning points based on second derivatives of the index curve

Table 1 Significant upturns (U) and downturns (D) of rabbit populations in the study period based on the second derivatives of abundance index (rate of change of the rate of change of the absolute abundance index)

| Region | 1978 | 1980 | 1982 | 1984 | 1988–1989 | 1990 | 1993 | 1996 | 1998–1999 |
|-----------------------------|------|------|------|------|-----------|------|------|------|-----------|
| All Spain | | D | U | U | D | | D | U | |
| Galicia (N Spain) | | | U | | | | | | D |
| Central Spain | D | | U | | D | | D | U | |
| Valencia + Murcia (E Spain) | | | | U | D | | D | D | |
| Andalucía (S Spain) | | | | | | D | U | D | |

absolute values of the abundance index were around 12–15% between consecutive years (Fig. 5a).

In eastern Spain, the pattern was different to the overall trend described. We observed a significant downturn in 1978, but the population showed a significant upturn in 1983 (Fig. 5b, Table 2). In the late 1980s, a significant downturn based on second derivatives of the index was observed, but this fact was not associated to a significant decline in the absolute values of the abundance index (Fig. 5b). Although not significant based on turning points (but this may reflect a very large confidence interval, see Fig. 5b), populations in eastern Spain suffered a strong decline in the absolute value of abundance index from 1998 to 2002 (Fig. 5b).

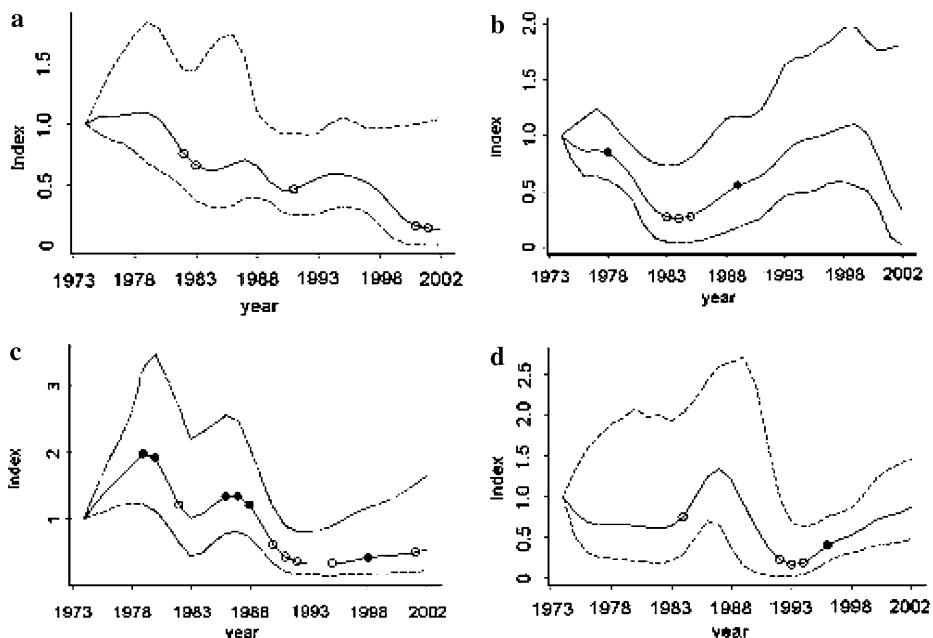


Fig. 5 Index curves (solid lines) for rabbit population trends in different areas of Spain from 1973 to 2002: Galicia, NW Spain (a), Levante, E Spain (b), central Spain (c) and Andalucía, South Spain (d). In all cases index curves were based on a GAM with 10 degrees of freedom. Dashed lines represent upper and lower 95% bootstrapped confidence intervals. Full circles correspond to significant negative turning points and empty dots represent significant positive turning points in second derivatives

Table 2 Threatened categories in the Spanish list of threatened species of 1990 (CNEA, Spanish acronym) and the type of program to be performed in each category

| Threatened categories CNEA 1990 | Government obligation |
|-----------------------------------|------------------------------|
| Endangered | Recovery program |
| Sensitive to habitat perturbation | Habitat conservation program |
| Vulnerable | Conservation program |
| Special interest | Management program |

In central Spain, the pattern was very similar to the overall pattern, although the first decline appeared slightly earlier (Fig. 5c). A decline of 82.56% was observed between the highest abundance in 1978 and the lowest in 1994, among the most marked declines across the country during the study period. We observed three significant downturns, in the years 1978, 1987 and 1995, whereas significant upturns were recorded in 1981, 1990–1992 and 2001 (Fig. 5c, Table 2). In contrast to the north-west and eastern regions, central populations showed some signs of recovery in the last 7 or 8 years, similar to the overall pattern.

In the south of Spain, rabbit populations appeared stable during the late 1970s (Fig. 5d). A significant upturn was detected in 1984–1985 (Fig. 5d, Table 2), when populations increased by 16–18%. A non-significant downturn occurred between 1987 and 1992 (Fig. 5d, Table 2), when populations crashed by 72%. In this calculation, the large confidence intervals likely precluded the detection of this decrease as significant in the analysis of second derivatives, a problem that was outlined in a similar study by Fewster et al. (2000). A significant upturn was recorded in 1995 and populations increased after this point, as in the case of central Spain.

In summary, rabbit population trends were similar country-wide, although the declines occurred at different moments depending on the region. Thus, some areas showed a large decline during the late 1980s and others showed declines in the last 5–6 years of the time series. Different regions also differed in the existence of previous declines before RHD outbreaks in the late 1980s.

Discussion

Hunting bags and GAM use in the analysis of population trends of game species

The study of population trends is a key element of the management of populations and a critical aspect of modern conservation biology (Geissler and Sauer 1990; Fewster et al. 2000). Several wild species are harvested or hunted by humans and records of these hunting activities potentially can be used when monitoring populations and conducting other ecological or environmental studies. An exemplary case is the use of fish catches in the analysis, forecast and management of fisheries (Hilborn and Walters 1992). Hunting bags also offer this opportunity, and they have been used for a variety of taxa to model population fluctuations, population trends and predator-prey dynamics (e.g., Cattadori and Hudson 1999; Kitson 2004).

Nevertheless, it is possible that hunting bag records are not good indicators of true population numbers or trends, and a direct validation has been called for. In some cases a good correlation has been shown between hunting bag data and true

population density or abundance (Royama 1992; Cattadori et al. 2003; Kitson 2004). Although a direct comparison of hunting bags and density of rabbits was not available, this is no reason to think that bags do not represent true numbers, or at least represent reliable population trends. Rabbit hunting method did not substantially change during the period of study (hunting with dogs and by individual hunters on foot), in contrast to hunting method in relation to other forms of small game such as the red-legged partridge (REGHAB 2002). We thus believe that the relationship between hunting bags and rabbit density did not differ between years. An interesting ‘ad hoc’ result that validated this source of data was the good correlation between significant population declines (turning points) and the appearance of RHD in multiple areas in Spain. RHD first appeared in some regions in 1988 (Argüello et al. 1988) and in the following five years most areas of Spain suffered the effects of this new disease (Blanco and Villafuerte 1993; Villafuerte et al. 1994; Cooke 2002). The significant turning points detected in our study were mainly located in the period 1987–1994 when declines of 50–90% were estimated in most areas, similar to data reported in local areas where the disease was studied (Peiró and Seva 1991; Blanco and Villafuerte 1993; Villafuerte et al. 1994).

Interestingly, although the greatest decline was observed during the period 1988–1989, a large crash was also observed in 1987–1988. These data may indicate that RHD virus was introduced to Spain a year before it was first recorded. The lack of suitable disease monitoring programs in Spain may have prevented the detection of the disease in the first epizootics. In France and central Europe, the first outbreaks were recorded in previous years (Cooke 2002) and it is therefore possible that this could also have been the case in Spain as suggested by our results.

In addition to demonstrating the value of using hunting bag data as a proxy for population numbers, we also highlighted the usefulness of GAMs for robust and flexible descriptions of population trends (see also Fewster et al. 2000; Siriwardena et al. 2000). The use of GAMs may enhance the scientific study of species status and conservation by including all possible functional relationships between population numbers and time.

Rabbit population decline and conservation

The wild rabbit is native to the Iberian Peninsula (Thompson and King 1989; Monnerot et al. 1994) and is an important prey item for many endangered predators, emphasizing the importance of its conservation. The rabbit is also a very important species for small game hunting in Spain (REGHAB 2002). Despite these facts, little effort has been made to conserve this species in Spain, where most action plans related to rabbit conservation have been developed within conservation programs for endemic endangered predators (MIMAM 1999, 2001; but see Calvete and Estrada 2004; Calvete et al. 2005).

Until the proclamation of the Law of Nature Conservation in 1989, which included the establishment of the National Threatened Species List (CNEA), Spain had no nationally organized concept of conservation. In 1990, the CNEA introduced three categories for classifying threat levels to native species that obliged the government to establish a particular conservation program for a species based on its threat category (Table 2). In 1992 the first CNEA was published and wild rabbit was listed as a “Least Concern” (LC) species (based on the Red Data Book for Spanish Mammals, Blanco and González 1992). Listing of taxa in this category implies that

there is no evidence that the survival of the species is threatened. Paradoxically, the best available evidence at that moment indicated that rabbit population crashes exceeding 80% had occurred in several regions of Spain (Peiró and Seva 1991). One year later, a technical report based on questionnaires was published suggesting that rabbit populations had declined by around 55% over a 5-year period and that this decline coincided with the first appearance of RHD in 1988 (Blanco and Villafuerte 1993).

At an international scale, the IUCN Red List System was established in 1994, which specified quantitative criteria for how taxa should be listed and conservation efforts initiated (IUCN 2001). Under these guidelines the IUCN stated that any taxon fitting at least one of five criteria should be included in one of the threatened categories (Critically Endangered, Endangered, Vulnerable; IUCN 2001). Moreover, the IUCN stated that the best available evidence about a species have to be used in order to list the species. In 2003, when the new version of the CNEA (CNEADI, in preparation) was proposed, only the studies of Peiró and Seva (1991) and Blanco and Villafuerte (1993) were available to evaluate rabbit status. Nevertheless, Criteria A of the CNEADI and the IUCN Red List System (population decline) require data from 50- and 10-year periods, respectively. Thus, although the available data were alarming, they were not sufficient to qualify rabbits for any category other than “Data Deficient” in the IUCN Red List system. Listing of taxa in this category indicates that more information is required and acknowledges the possibility that future research will show that a threatened classification is appropriate. Surprisingly, the rabbit has again been proposed as a LC species in the CNEADI. A taxon is LC when it has been evaluated against the criteria and does not qualify for any of the threatened categories (IUCN 2001).

The IUCN states that it is important to make positive use of whatever data are available. In many cases great care should be exercised in choosing between ‘Data Deficient’ and a threatened status (IUCN 2001). Our study is the first scientific attempt to quantify rabbit population trends in Spain over the last 30 years, and the data are clear and relevant: wild rabbits have suffered a major national decline of around 70%, with values of up to 90% observed in some areas. Indeed, such a strong decline may be considered as catastrophic (Reed et al. 2003), which greatly increases the probability of extinction of these populations (Lande 1993; Reed et al. 2003). Following the criteria of the IUCN Red List System, our analysis indicates a population size reduction of 42–49% over most 10-year periods within the 30 year-period of the present study. Thus, our result proves that the rabbit meets Criteria A4 and should be listed as Vulnerable. According to the CNEADI requirement that data cover a period of more than 50 years, our study period is too short; however, if experts were in agreement about rabbit status, the species could also be listed as VU and as such, the Spanish government would be obliged to establish a conservation program (Table 2). Nevertheless, it is important to emphasize that a taxon may require conservation action even if it is not officially listed as threatened.

The lack of a nationwide conservation program for wild rabbit in Spain is probably one of the most paradoxical conservation issues in Europe, and possibly the world. Similar to the declines observed in Spain, the appearance of RHD in Australia and New Zealand in 1995 caused large population crashes of 40–95% (Neave 1999; Cooke 2002). In contrast to the Spanish situation, researchers, managers and conservationists in those countries all agreed upon the usefulness of national monitoring programs and research on rabbits. This attitude promoted governments to

perform such monitoring not only for studying population trends, but also for the detection and study of RHD outbreaks (Neave 1999; Cooke 2002; Henzell et al. 2002). Furthermore, it must be noted that, in contrast to Spain, the rabbit is considered a major pest in the southern hemisphere, where it has been introduced and has caused significant environmental damage. The large discrepancy between the Spanish and Australian attitudes to the researching and monitoring of rabbits highlights how similar situations can elicit very different conservation responses.

The major declines observed in Spain give rise to a general question: why is the wild rabbit not a protected species in Spain? The case of rabbits in Spain is a good example of the constraints faced by conservationists in most countries, where in addition to demographic baseline data, conservation practices are dictated mainly by socio-economic constraints including political trade-offs, ‘lobby’ pressures and traditional management (Kellert 1985; Pullin and Knight 2001). Since the IUCN World Conservation Strategy (1980), the management of species has shifted from a strict ‘conservationist’ view to one where people’s perceptions and attitudes play a key role in conservation decisions (Bandara and Tisdell 2003). Within this new paradigm, even small but important stakeholder groups may exert a strong influence on conservation decisions (Kellert 1985).

Despite the decrease in the economic value of rabbit hunting in the last decades (perhaps as a consequence of rabbit decline), rabbits continue to be socially important. Rabbit hunting is mainly carried out by municipal and local associations of hunters who do not have enough economic resources to access other small game hunting practices, such as red-legged partridge hunting (Bernabeu 2000). Therefore, rabbit is the only hunting species for a large proportion of hunters. Moreover, many of these hunters consider rabbit hunting a traditional activity with large emotional value (REGHAB 2002). The hunter collective represents a very important social force in Spain; for instance, 80% of the country is covered by hunting lands (REGHAB 2002) and around 1.3 million people are linked to game activities, with most of them linked to rabbit hunting (REGHAB 2002; Angulo and Villafuerte 2003).

It is clear that politicians are influenced by hunter demands or opinions about wildlife conservation or management. Although in the last decades the conservation movement has strengthened in Spain, its political influence remains low, especially in rural areas (Kellert 1985; Bandara and Tisdell 2003). It is also clear that any conservation measures that may reduce traditional hunting activities, especially actions related to the conservation of game species, will face strong opposition from hunters and politicians, and so managers or conservationists may be reluctant to implement such measures.

Furthermore, the Spanish Hunters Federation and other hunter associations often make economic contributions to researchers who study rabbits and other game species. Such contributions are good for conservation biology, but could be questionable in instances where the interests of multiple lobby groups are in opposition. Unfortunately, we feel that most decisions regarding rabbit conservation in Spain could be tainted by such negative feedback between research, management and funding sources.

The sociological scenario for rabbit conservation in Spain is therefore very complex, with politicians, hunters, conservationists and other social forces playing distinct roles. Similar social or political interference in conservation plans has been observed elsewhere. Perhaps the best-known example in recent decades has been the

restocking of wolf populations in Yellowstone National Park, USA (Wilson 1997; Bangs et al. 1998). Conservationists and managers sought the recovery of the park community structure prior to the depletion of the wolf population by man. In contrast, landowners, mainly devoted to cattle raising, were very reluctant and opposed to attempts to bolster the population of such a predator. After much heated debate, politicians and managers agreed to re-establish wolves based on ecological principles, but assuming a certain social cost (Wilson 1997). This example shows how conservation priorities may overcome social opposition when biological reasoning prevails. In some circumstances biological reasoning may not be as useful, and a strong opposition may impede implementation of conservation actions or reduce the efficacy of whatever action is taken. For example, the restocking of a species such as the wolf in areas with high cattle interests may lead to landowners using poison, negatively affecting both wolves (the target of the management action) and other species of conservation concern (e.g., other carnivores, raptors, etc.). We thus advocate a balance between social and biological reasoning.

In conclusion, we call for the urgent development of a national conservation plan for rabbits in Spain, independent of the Iberian lynx and Imperial eagle recovery programs. We want to emphasize that the conservation of rabbits cannot be impeded for sociological reasons or to accommodate any particular lobby group. This conservation plan does not need to be restricted to the protection of rabbits, which may elicit strong opposition from hunters and farmers; rather, it should be based on an adaptive approach (MacNab 1983; Parma et al. 1998). Within this framework, management actions should be based on the particular circumstances of each region, including social opposition in areas where rabbits cause significant crop damage. We also wish to emphasize the need to make positive use of whatever data are available (Pullin and Knight 2001), and advocate the use of scientific methods and standard scientific procedures when making conservation decisions, especially when classifying species into conservation categories.

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Identifying core areas in a species' range using temporal suitability analysis: an example using little bustards *Tetrax tetrax* L. in Spain

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Abstract Variations in habitat quality impact on breeding success, leading to strong selection pressure for the best sites to be occupied first during a population increase and last during a decline. Coupled with dispersal and metapopulation processes, the result is that snapshot surveys of wildlife distributions may fail to reveal core areas that conservation seeks to protect. At a local scale, territory occupancy is a good indicator of quality but data are not readily available to assess occupancy for rarer species, in remote areas, and over large spatial extents. We introduce temporal suitability analysis as a way to generate an analogue of occupancy from a single survey and illustrate it using data on the little bustard in Spain. We first used Generalised Additive Modelling (GAM) to build a predictive distribution model using Geographic Information System (GIS) coverages and satellite imagery, and then applied the model retrospectively to a time series of satellite images to produce one distribution map for each year. These annual maps differed in the extent of Spain predicted as suitable for little bustards. By overlaying the maps, we identified areas predicted as suitable in one to n years. We show that this temporal suitability map correlates with a conventional habitat suitability map based on a single year but contains extra information on hierarchical use of habitats and the lag between suitability and use. The technique may be applied at a variety of spatial scales to reveal changes in expected occupancy as land use or external factors determining land cover types vary over time.

Keywords Distribution modelling · GAM · Habitat selection · NDVI time series · Occupancy · Steppe birds

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Abbreviations

| | |
|-------|--------------------------------------------|
| AUC | Area under the curve (used for ROC plots) |
| AVHRR | Advanced Very High Resolution Radiometer |
| DTM | Digital terrain model |
| GAM | Generalised Additive Modelling |
| GLM | Generalised Linear Modelling |
| GIS | Geographic Information System |
| HSI | Habitat Suitability Index |
| NDVI | Normalised Difference Vegetation Index |
| ROC | Receiver Operating Characteristics (curve) |

Introduction

Spatial variation in habitat suitability and its effect on breeding success (e.g., Newton 1989) combine to make species' distributions non-random and dynamically linked to population size. There is strong selection pressure for the best sites to be occupied first and competition for good sites may affect arrival times at breeding sites and cause partial migration (Kokko 1999). Established ecological theory tells us that suboptimal areas are only used when competitive exclusion drives often lower quality individuals out at high population densities, as described by the "ideal free distribution" (Fretwell and Lucas 1970) and the "buffer effect" (Brown 1969). Through source-sink dynamics and the rescue effect, poorer quality sites may themselves not be self-sustaining, instead relying on immigration from the better habitat patches where productivity is high (Brown and Kodric-Brown 1977; Pulliam 1988; Hanski 1999). Suboptimal areas may even reach higher population densities than better sites because lower quality individuals are poor resource defenders (Van Horne 1983). The result of these interacting ecological processes is that it is not easy to identify core areas within a species' range from distribution data, especially from snapshot surveys of wildlife. By core areas, we mean those locations on which the sustainability of the population depends, which must be key targets for conservation.

Sergio and Newton (2003) suggested that the best territories may be identified from occupancy, that is, how often they are used. In their review of studies on territorial birds, Sergio and Newton (2003) found that occupancy was always non-random and always correlated with territory quality. They argue that occupancy may be an efficient way to identify the best sites because national agencies may already have the data from population monitoring surveys. Unfortunately, this will not always be the case, particularly in remoter, poorly studied areas, perhaps where conservation prioritisation is most pressing. Often, a single snapshot survey is all that can be arranged to gather information on a species, perhaps running over several years in different parts of range. The long runs of data needed to assess occupancy may thus be lacking or cost too much and take too long to assemble for some species and at large spatial scales.

It has long been recognised that sample surveys may be enhanced through statistical modelling that effectively plugs the gaps in a distribution that arise from poor or uneven coverage (Nichols 1989; Osborne and Tigar 1992; Buckland and Elston

1993). Such distribution modelling has grown in sophistication as statistical methods, Geographical Information Systems (GIS) and remote sensing technologies have advanced (Guisan and Zimmermann 2000; Guisan et al. 2002). These modelling approaches rely on extrapolating spatially the known associations between species occurrences and habitat features, now often in the form of remotely sensed data. We reasoned that it would be equally valid to extrapolate temporally as well as spatially given certain assumptions. If a number of predictive distribution maps could be derived from a time-series of satellite images, then combining them could provide an analogue of occupancy. This approach would yield from a single snapshot survey a predicted pattern of habitat suitability (and hence predicted occupancy) over time which we call temporal suitability analysis. We explore this idea here by using data on little bustards *Tetrax tetrax* L. from Spain.

The little bustard is a near-threatened species (Red List category LR/nt—IUCN 2003), considered vulnerable in Europe. It is listed on Annex 1 of the European Union (EU) Wild Birds Directive and Appendix II of the Bern Convention because it is scarcely distributed in the EU and has experienced a heavy population decline during recent years. Its population trend is still downward and it nearly qualifies for listing under Red List criteria A1cd + 2cd (IUCN 2003). Little bustards occur as two widely separated populations with an eastern and a western distribution. They occur in the east in Russia, Ukraine, Kyrgyzstan, Kazakhstan, China, Iran and Turkey, where they number fewer than 40,000 individuals. The western population in Spain, Portugal, France and Italy has at least 200,000 individuals, of which more than 95% are in Spain, which therefore has responsibility for the bulk of the world's population. Originally a bird of dry grasslands, European little bustards mostly inhabit extensive dry cereal crops and pastoral lands with a high diversity of ground cover (e.g., Silva et al. 2004). The species has declined since the 19th century and become extinct in 14 countries, including 11 in Europe. The main causes of decline have been agricultural intensification (Wolff et al. 2001), the planting of monocultures, use of irrigation (Brotons et al. 2004) and in some places, afforestation, shooting and pesticides. The vagueness of population estimates (e.g., Spain has 100,000–200,000 displaying males and an unknown number of females) stresses the difficulty of accurately surveying little bustard populations, and make it an appropriate species for indirect approaches.

Methods

The basis of our approach to distribution modelling and the data sets are described in detail in Suárez-Seoane et al. (2002). We describe here only the additional details required to extend the analysis through time. The satellite data were obtained from the archive of Advanced Very High Resolution Radiometer (AVHRR) imagery held at the Natural Environment Research Council's Satellite Receiving Station in Dundee, Scotland and were processed by the Remote Sensing Group at the Plymouth Marine Laboratory, England. Data were obtained for 1983, 1985, 1990, 1993, 1996 and 1999, covering the whole of Spain at 1 km² resolution. Following Suárez-Seoane et al. (2002) we extracted monthly maximum value composites of Normalised Difference Vegetation Index (NDVI) data from the AVHRR imagery using only images that passed our quality control checks. Although NDVI images can normally be used without calibration, we found a gradual “brightening” over the

long time series examined which was entirely due to filter degradation. The visible channels (i.e., channels 1 and 2 which are used to calculate NDVI) were therefore corrected for filter degradation using the Rao and Chen (1995) approach together with updates from the Dundee Satellite Receiving Station web site (<http://www.sat.dundee.ac.uk/cal>).

In previously using NDVI data for a single year, we found that regional differences in the timing of agricultural operations made use of monthly comparisons difficult. As a solution we extracted a series of principal components from the monthly data and used these in the modelling (Suárez-Seoane et al. 2002). When using data over several years, however, this approach proved unsatisfactory as peaks in biomass shift between years for any single location. To overcome this problem, we noted the periods during which biomass highs and lows typically occurred in the year and denoted these as seasons, combining the monthly data to provide the basic NDVI variables. Further variables were derived by calculating the differences in biomass between these seasons. Thus, for example, the variable for spring growth was derived as the difference between spring and winter, and reflects the amount of fresh growth in the spring. The derived NDVI variables used are summarised in Table 1.

We retained the GIS data layers (topography, roads, towns and rivers) used by Suárez-Seoane et al. (2002) since they are integral to the models. Ideally, they should have been obtained for each of the 6 years for which satellite imagery were available, but this was not possible as the information was not readily available, if it exists at all. The assumption in using the same layers in all the models here is that

Table 1 Variables used for modelling the occurrence of little bustards in Spain derived from AVHRR imagery and GIS data layers

| Variable | Definition |
|-----------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Maximum NDVI (MAX) | Maximum of the 12 monthly NDVI values for each pixel |
| Minimum NDVI (MIN) | Minimum of the 12 monthly NDVI values for each pixel |
| Mean NDVI (MEAN) | Mean of the 12 monthly NDVI values for each pixel |
| Summer NDVI (SUMMER) | Minimum of NDVI for July and August |
| Winter NDVI (WINTER) | Minimum of NDVI for November and December |
| Spring growth (GROWTH) | Maximum of April or May minus Summer NDVI |
| Autumn loss (LOSS) | Summer NDVI minus minimum of September and October |
| Altitude (ALT) | Mean altitude within a 5×5 array of 200 m pixels |
| Topographic variability 10 (TOPOV10) | Variation in altitude in a 5×5 pixel array of 200 m pixels, where altitude is measured to 10 m vertical resolution. Calculated as $\text{TOPOV10} = (n-1)/(p-1)$ where n = no. of different altitude classes in the array and p = no. of pixels in the array (i.e., 25) |
| Road density (ROADDEN) | Proportion of 200 m pixels in a 5×5 array containing roads |
| Road distance (ROADDIST) | Distance in km to the nearest 200 m pixel containing roads. Calculated at 200 m resolution and averaged to 1 km^2 |
| Town density (TOWNDEN) | Proportion of 200 m pixels in 5×5 array containing buildings or large built structures such as airfields |
| Town distance (TOWNDIST) | Distance in km to the nearest 200 m pixel containing buildings or large built structures such as airfields. Calculated at 200 m resolution and averaged to 1 km^2 |
| River density (RIVDEN) | Proportion of 200 m pixels in a 5×5 array containing rivers |
| River distance (RIVDIST) | Distance in km to the nearest 200 m pixel containing rivers. Calculated at 200 m resolution and averaged to 1 km^2 |

they have not changed significantly over the period 1983–1999. This is unlikely to be true for the road network and the sizes of towns but the magnitude of their change is likely to be much less than that for vegetation, especially on agricultural land. We therefore regard the assumption as reasonable.

The base model was built using 486 records of little bustard occurrence gathered during 1998–2001, matched with an equal number of locations recording absence, randomly drawn from the database of surveyed points. The bird data were modelled using the 1999 satellite imagery and the GIS data layers (Table 1) through Generalised Additive Modelling (GAM) using S-plus 2000 (see Venables and Ripley 1999) and GRASP (Lehmann et al. 2002). We fitted cubic splines with four degrees of freedom to each predictor, using a logit link and binomial error structure. Parsimonious models were generated using backwards selection with a Chi-squared value of 0.05 (Pearce and Ferrier 2000a) for the variable to remain in the equation. We tested whether each smoothed term was significant over a linear model and replaced non-significant smooths with linear terms to prevent over-fitting to the data. A likelihood ratio test was used to assess the contribution of each variable to the final equation (Venables and Ripley 1999). We assessed the predictive performance of the model using 10-fold cross validation (see Suárez-Seoane et al. 2002) and the area under the ROC curve (AUC) (Beck and Shultz 1986; Fielding and Bell 1997; Osborne et al. 2001).

Once the base model for 1999 had been derived, we substituted the NDVI values from previous years into the model and re-ran the predictions. Predictions for each year were transformed into a probability map by generating a look-up table and passing it to Idrisi 32.11 (Eastman 2000) for extrapolation across Spain (procedure in Suárez-Seoane et al. 2002). Each map consisted of a habitat suitability index (HSI) with a (probability) scale from 0 to 1. The six yearly maps were then thresholded at 0.7 probability to produce binary images of “good” areas. These binary images were overlaid and the number of years each pixel was defined as suitable recorded to produce the temporal map of suitability. For presentational purposes (but not for analysis) the map was subjected to a repeat-pass modal filter to smooth it (see examples in Fig. 1).

We investigated the broad habitat types within each category of the temporal suitability map by overlaying it on the CORINE land cover map for Spain. Although our ground-truthing of this map showed it to be a broad-brush classification (unpublished data) there is no reason to expect its biases to correlate with our temporal suitability categories. As a precaution, however, we also examined the habitat types used in Madrid Province based on the more accurate land cover map, at 1:50,000 scale, from the Regional Government.

Results

The base model for 1999 used six explanatory variables (Table 2) and fitted the data well (ROC AUC = 0.92, $P < 0.001$) and had good predictive power (cross-validated ROC AUC = 0.90, $P < 0.001$). It featured two NDVI variables (annual mean biomass and summer peak), two topographic variables and two distance variables indicating an avoidance of towns and roads. We generated the distribution map for 1999 by thresholding the probabilities for each 1 km² pixel at 0.7 to make a binary image (lower right of Fig. 1). Good areas for the little bustard are predicted to occur

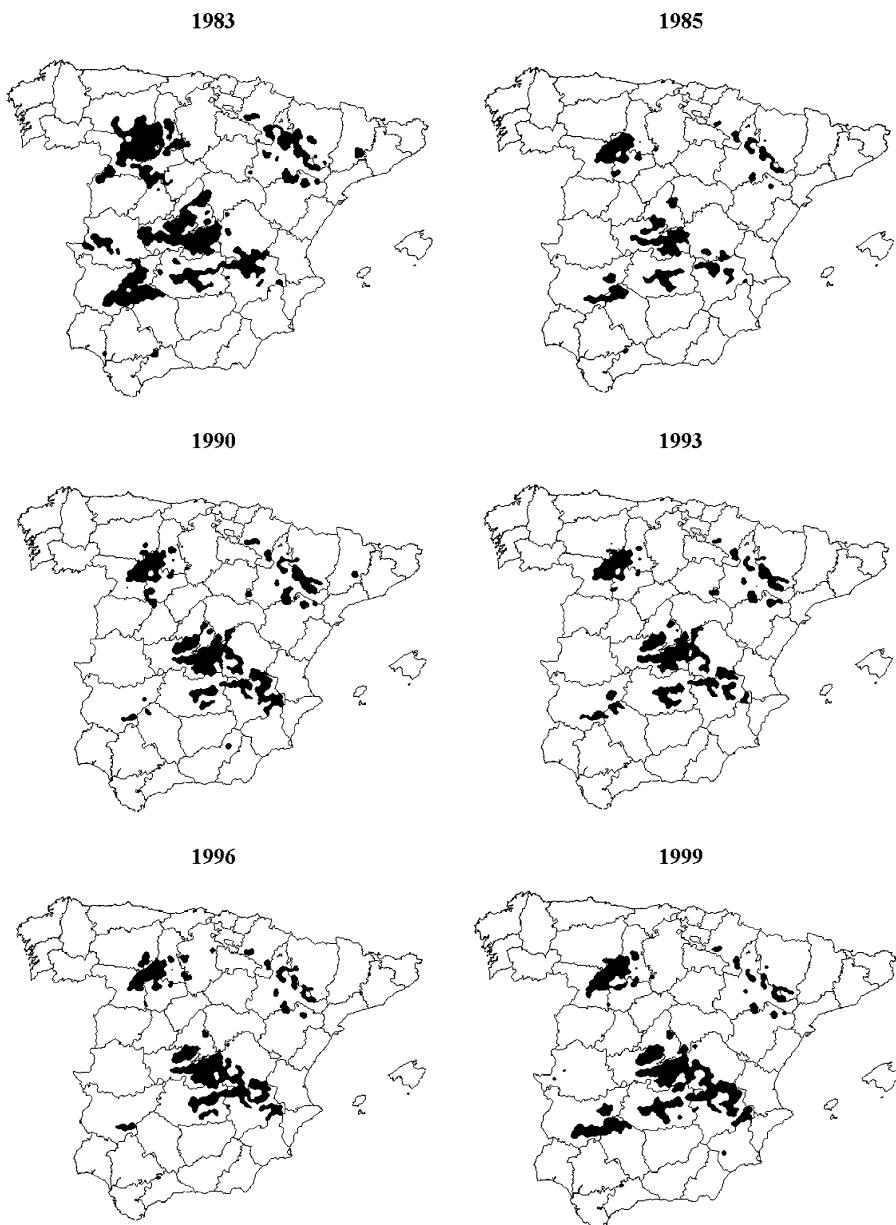


Fig. 1 Habitat suitability maps for the little bustard in 6 years showing only areas with an HSI > 0.7

in several main nucleus: the Ebro Valley, Tierra de Campos (Castilla-León), La Serena (Badajoz)-Northern Córdoba, Calatrava (Ciudad Real) and the axis Madrid-Toledo-Southern Cuenca-Northern Badajoz, conforming to existing knowledge on the species (Martí and del Moral 2003). More peripheral areas that hold fewer birds such as NW Spain are deliberately excluded by the thresholding to focus on the main concentrations.

Table 2 Significant variables in the final Generalised Additive Model predicting little bustard occurrence in Spain during the 1999 base year. The column “Term” indicates whether a non-parametric smoothing spline or a linear term was used in the model. Linear terms are further marked as positive or negative

| Variable | Term | F-test | Probability |
|----------|------------|--------|-------------|
| Mean | Smooth | 4.41 | 0.002 |
| Summer | Smooth | 13.55 | <0.001 |
| Topov10 | Linear (-) | 32.18 | <0.001 |
| Altitude | Smooth | 11.45 | <0.001 |
| Towndist | Linear (+) | 6.41 | 0.012 |
| Roaddist | Linear (+) | 12.09 | <0.001 |

When the 1999 base model was used with NDVI imagery from previous years it generated the annual distribution maps in Fig. 1 (all subjected to modal filtering to improve presentation). Note that the same broad areas of Spain are predicted as being suitable but that the extent of suitable habitat in each varies between years (1983, for example, had a larger extent of land defined as suitable). The data do not show a monotonic change in extent of suitable habitat but variations between years that presumably relate to factors such as climate. Superimposing the unsmoothed data used to make the maps in Fig. 1 and then smoothing the result gives the temporal suitability map with a suitability scale of 1–6 years (Fig. 2).

An analysis of the land cover types in areas with different temporal suitabilities shows a strong selection of non-irrigated cultivation (Table 3; Fig. 3). The patterns were broadly similar for Madrid Province and the whole of Spain with non-irrigated

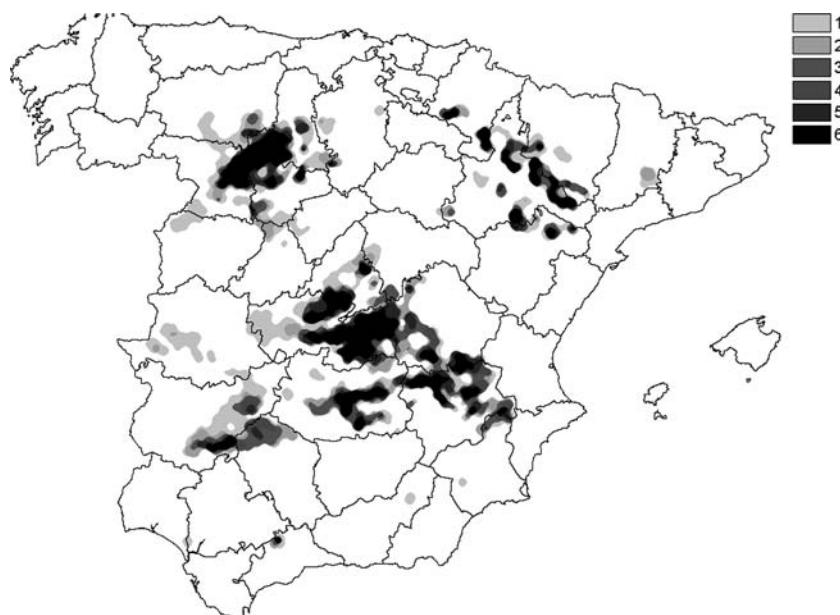


Fig. 2 Temporal suitability map for the little bustard in Spain showing the number of years of suitability (range 0–6 years)

land forming around 60–70% of the most frequently suitable areas, declining to around 30% of all areas suitable in only 1 year. The data for Madrid Province are notably different from Spain as a whole in having more little bustards associated with urban areas and living closer to wooded land (Table 3). The latter reflects the greater degree of habitat fragmentation around the capital city and consequent mixed pixels at 1 km² resolution that contain both suitable habitat and other (dominant) land use features.

To judge whether temporal suitability modelling provided additional information to the HSI derived from the single 1999 base data, we carried out two further tests. First, we plotted the percentage of pixels for each 0.1 class in the HSI against the no. of years of suitability (Fig. 4). The results showed that the 0.7–0.8 class from the 1999 map was pivotal and rather evenly spread across the 1–6 years suitability. In the 0.8–0.9 class, 61% of pixels were suitable in 6 years, and in the 0.5–0.6 class, 63% were unsuitable in all years. Although the average correspondence between HSI interval from a single year's model and the number of suitable years was good, there was considerable spread and every interval had at least one pixel in each year class (where possible—see Discussion). In the second test, we tried to identify the nature of the difference in the information obtained from temporal suitability modelling and the single GAM model. Starting with the 2 × 2 confusion matrix from the GAM model, we examined the results of the temporal suitability approach for locations either correctly or incorrectly classified as occupied or unoccupied by the GAM. For locations predicted as suitable, we could find no significant difference in temporal suitability scores between places that were actually occupied or vacant (log-likelihood ratio test, $\chi^2 = 3.58$, DF = 3, $P = 0.31$). There was, however, a highly significant difference between temporal suitability scores at unsuitable sites that were actually occupied and those that were vacant (log-likelihood ratio test, $\chi^2 = 114.71$, DF = 3, $P < 0.001$). For example, while 92.9% (408/439) of unsuitable, unoccupied sites had a temporal suitability score of zero, for sites that were predicted unsuitable in the GAM but that were actually used, only 52.6% (81/154) scored zero. We therefore conclude that temporal suitability mapping provides extra information for the data set examined, especially on the locations of sites that the single year GAM predicted as unsuitable yet were occupied.

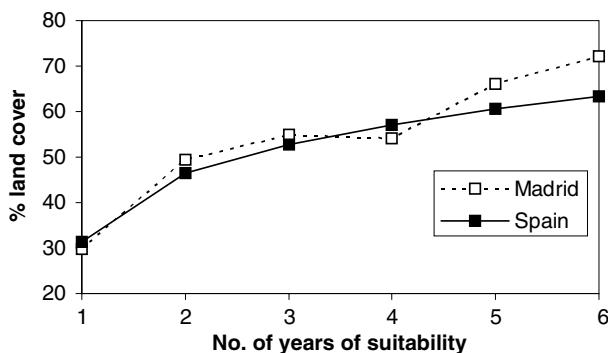
Discussion

Species modelling using GLM/GAM approaches (e.g., Guisan et al. 2002) has largely focussed on the spatial dimension to date. The recent literature provides examples of diverse applications to plants (Zimmermann and Kienast 1999; Heegard et al. 2001), birds (Suárez-Seoane et al. 2002; Seoane et al. 2004), mammals (Jaberg and Guisan 2001), reptiles (Guisan and Hofer 2003), invertebrates (Maggini et al. 2002) and diseases (Wint et al. 2002), and the technique has provided valuable insights into factors limiting species' ranges such as competition (e.g., Leathwick and Austin 2001; Groves et al. 2003). (For older references, see Guisan and Zimmermann 2000). Applied ecology, however, often requires predictions to be made over time as well as space and aside from climate change modelling (e.g., Teixeira and Arntzen 2002) has been addressed less often (but see Brotons et al. 2004 for an exception). Any modelling approach is unreliable when predictions are made beyond the data domain since the form of the relationship between response and

Table 3 Percentage composition of land cover types in areas predicted to be suitable for little bustards in 1, 2...6 years. The upper table for the whole of Spain is derived from the CORINE database at 1:100,000 whereas the lower table is for Madrid Province only based on the Regional Government land cover map at 1:50,000

| | All Spain | Irrigated cultivation | Non-irrigated cultivation | Pasture/ grassland mosaics | Agricultural mosaics | Scrub | Vine/ tree crops | Agro-forestry | Deciduous forest | Evergreen forest | Coniferous forest | Mixed forest | Rocky areas | Urban areas | Reservoirs |
|---------------|-----------|-----------------------|---------------------------|----------------------------|----------------------|-------|------------------|---------------|------------------|------------------|-------------------|--------------|-------------|-------------|------------|
| 1 | 5.0 | 31.4 | 7.9 | 11.5 | 17.7 | 5.1 | 9.4 | 4.6 | 0 | 4.1 | 0.3 | 0.3 | 1.6 | 0.5 | 0.6 |
| 2 | 4.5 | 46.5 | 5.5 | 12.0 | 11.7 | 6.3 | 6.3 | 1.6 | 0 | 2.9 | 0.1 | 0.1 | 1.2 | 0.4 | 0.8 |
| 3 | 2.9 | 52.8 | 6.2 | 11.4 | 9.3 | 6.4 | 5.4 | 1.0 | 0 | 1.8 | 0.1 | 0.1 | 1.1 | 0.6 | 1.0 |
| 4 | 1.9 | 57.1 | 5.2 | 12.1 | 8.5 | 6.7 | 3.5 | 0.6 | 0 | 1.6 | 0.0 | 0.0 | 1.0 | 0.5 | 1.1 |
| 5 | 2.0 | 60.5 | 3.4 | 12.6 | 7.3 | 6.3 | 3.2 | 0.4 | 0 | 1.4 | 0.0 | 0.0 | 1.3 | 0.3 | 1.2 |
| 6 | 0.9 | 63.4 | 2.8 | 14.0 | 6.7 | 6.1 | 2.6 | 0.2 | 0 | 1.6 | 0.0 | 0.0 | 0.8 | 0.1 | 0.7 |
| <i>Madrid</i> | | | | | | | | | | | | | | | |
| 1 | 5.3 | 29.8 | 3.5 | 4.0 | 11.0 | 0 | 0 | 1.2 | 25.0 | 4.9 | 0 | 0 | 0 | 14.8 | 0.5 |
| 2 | 3.5 | 49.4 | 3.8 | 5.5 | 9.3 | 0 | 0 | 1.7 | 8.4 | 3.2 | 0 | 0 | 0 | 14.5 | 0.9 |
| 3 | 3.7 | 54.9 | 3.5 | 3.2 | 10.6 | 0 | 0 | 2.0 | 7.8 | 1.7 | 0 | 0 | 0 | 12.4 | 0.3 |
| 4 | 3.9 | 54.1 | 1.1 | 8.4 | 10.4 | 0 | 0 | 2.2 | 4.2 | 2.0 | 0 | 0 | 0 | 13.2 | 0.6 |
| 5 | 1.5 | 66.1 | 1.0 | 10.1 | 9.4 | 0 | 0 | 1.0 | 1.5 | 1.5 | 0 | 0 | 0 | 7.9 | 0.0 |
| 6 | 1.5 | 72.1 | 0.4 | 11.5 | 7.6 | 0 | 0 | 0.6 | 1.7 | 1.2 | 0 | 0 | 0 | 3.2 | 0.3 |

Fig. 3 Non-irrigated arable land as a percentage of land cover types in areas predicted to be suitable for little bustards in 1–6 years



predictors is unknown. There is also doubt whether the correlation structure that these models uncover is sufficiently robust and process-based to survive transfer to new situations. This has led some researchers (e.g., Fielding and Haworth 1995; Whittingham et al. 2003) to question whether spatial models have sufficient generality for application to new areas. As Guisan and Zimmermann (2000) put it, empirical or statistical models often sacrifice generality for precision and reality. Similar caution is clearly needed in extending predictive models through time, but the underlying logic is no different. In our approach, we sought to find a way to mimic occupancy that Sergio and Newton (2003) have found to be a good indicator of territory quality. Spatial models can accurately predict the whereabouts of suitable habitat and can thus predict potential distributions. They even have some advantages over raw distribution data, for example in locating vacant habitat patches (Suárez-Seoane et al. 2002) that are crucial in metapopulation dynamics (Hanski 1999). Given that evolution should favour individuals occupying the best habitats, there should be a relationship between occupancy and habitat suitability as predicted from spatial models. By examining predicted suitability over a number of years, we are generating a pseudo-occupancy map that may help to locate core areas.

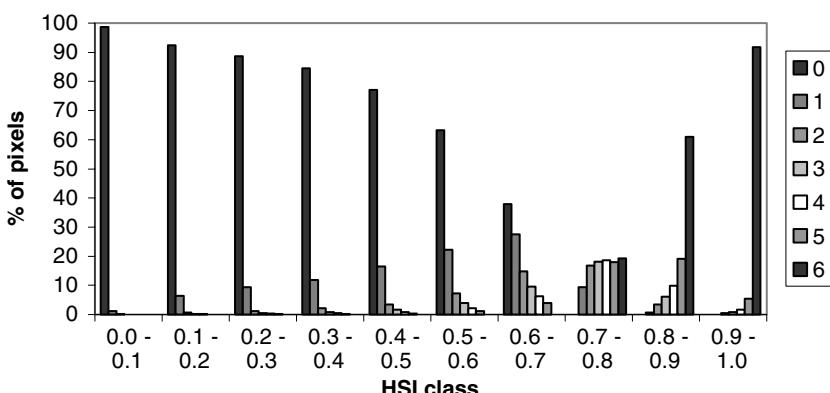


Fig. 4 Relationship between Habitat Suitability Index (HSI) class from the 1999 base model and the no. of years of suitability from temporal suitability analysis (range 0–6 years)

There is, however, a key difference between our approach and mapping occupancy directly. Occupancy *sensu* Sergio and Newton (2003) relies on repeated observations of the birds themselves whereas we focus on habitat correlates of occurrence. This distinction may not be trivial in interpreting the results. For example, the temporal suitability map in Fig. 2 shows distinct core areas surround by contiguous areas of less frequent suitability, reminiscent of a buffer effect (Brown 1969) where areas are occupied hierarchically with suboptimal individuals waiting in the neighbourhood of good habitat (Krebs 1971). Rather than showing a dynamic distribution as a result of changes in population density, however, we suggest that Fig. 2 might predict likelihood of successful breeding through habitat suitability. This is a testable prediction but not one that we know has been examined.

Another area for future study is how best to choose the threshold needed to produce binary presence-absence maps from the probability scale that logistic GLM/GAM models generate. As Pearce and Ferrier (2000b) note, the choice of a decision threshold is often rather arbitrary and usually partly based on value judgements regarding the consequences of correct and incorrect decisions. The traditional objective approach has been to use the prevalence in the data set (i.e., the ratio of presence to absence points) to set the threshold (Fielding and Bell 1997). Others have preferred to calculate an optimum based on minimising false negatives and false positives (Manel et al. 2001, Brotons et al. 2004) or maximising the percentage correctly classified points in the predictions (Suárez-Seoane et al. 2002). In a previous study we found that the optimum threshold for simply separating presence from absence points for the little bustard was 0.58 (Suárez-Seoane et al. 2002) and this sets the lower threshold for defining core areas. Here we chose 0.7 because it gave a sensible discrimination between the better and poorer areas. However, the definition of “best” areas for conservation requires value judgements and no single threshold should be used without question. Since we overlaid the annual binary maps to produce the temporal suitability map, changing the threshold would alter the extent of the total area defined as core and move the boundaries between adjoining classes of suitability.

We tested how much extra information temporal suitability analysis yields over conventional habitat suitability modelling by examining the percentage of pixels in each 0.1 width HSI class from the 1999 base model that were classed as suitable for 0–6 years (Fig. 4). Since we thresholded the model at 0.7 and defined all areas with higher probabilities as suitable, it was not possible for probability intervals over 0.7 to score less than one in this analysis (which would be for 1999). Similarly, probabilities less than 0.7 could not score higher than 5 years of suitability. Aside from this, the proportions of pixels in the HSI classes were unconstrained. For our data set, it was clear that the temporal analysis provided new information despite a general tendency for the single year HSI to correlate with the no. of years of suitability, particularly at the extremes of both scales (e.g., an HSI of 0.9–1.0 largely corresponded with 6 years of suitability, and an HSI < 0.1 almost uniquely indicated areas that were never suitable). This general correlation is to be expected in any species that occupies the same broad areas year to year, and the variations are due in our case to the inter-annual variations in the pattern of NDVI across Spain. We would expect, however, the relationship between HSI and temporal suitability to vary between data sets.

In our case, we were able to show that temporal suitability modelling helped to explain the false negatives that often arise in distribution modelling. For the little

bustard, false negative sites tended to be those that were suitable in other years, even though the GAM for 1999 regarded them as unsuitable. Temporal suitability modelling thus detects the lag in species responses to change. Interestingly, we could not detect an explanation for false positives, the converse situation. Single year GAMs often identify as suitable a number of sites with proven absence. We hypothesised that these might again arise due to a lag, i.e., that although suitable now, they were too infrequently suitable in the past to be occupied. There was only a very slight (non-significant) tendency for this to be true, for example, 68.1% of false-positive sites were suitable in five or more years compared with 79.7% of sites correctly identified as occupied. We thus conclude that inter-annual variations in NDVI can only weakly explain the difference between occupied and unoccupied suitable sites.

Temporal suitability analysis appears to provide information on habitat use (or predicted reproductive success within habitat type) that accords with what is known of the little bustard's biology. Our analysis showed that around 63% of the most frequently suitable sites occurred on non-irrigated cultivation with a further 14% on agricultural mosaics. Crop irrigation is a cause of decline in little bustards (Brotons et al. 2004) and it is noteworthy that irrigated lands formed less than 1% of areas suitable over 6 years. The percentage formed by irrigated land only increased to 5% for areas suitable for a single year even though non-irrigated cultivation now formed just 31%, i.e., half of the figure for areas suitable for 6 years. This suggests that habitats other than irrigated land are preferred when non-irrigated cultivation is occupied. In comparing areas suitable for only one as opposed to 6 years, we found the largest differences in land use composition to be for grasslands (8% vs. 3%), scrub (18% vs. 7%), agro-forestry (9% vs. 3%), deciduous forests (5% vs. 0%) and coniferous forests (4% vs. 2%), the latter two being explained by the presence of small areas of non-forest habitats in 1 km² pixels dominated by trees. Little bustards are known to occupy more mosaic habitats and at a finer scale than the related great bustard *Otis tarda* L.

In conclusion, this paper introduces temporal suitability analysis as an analogue of occupancy to yield extra information on habitat selection and to identify core areas within a species' range. Such areas are those that are suitable over a long time period despite environmental changes. We do regard the approach as experimental and urge other researchers to explore its use on other species and in other situations, especially if real data on occupancy are known. The technique is likely to be of most use in examining routinely occurring changes such as may occur within the farming cycle, or in habitats subject to natural burning. Choice of the time frame examined and the spatial scale used are likely to be important and related issues. Coarse resolution imagery is blind to fine scale habitat changes and longer time series are likely to show general variations in, for example, green biomass, rather than crop rotations. On the other hand, fine scale imagery could be valuable in capturing inter-annual variations in cropping that make fields suitable 1 year and not the next.

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Discovery of a regular nesting area of loggerhead turtle *Caretta caretta* in southern Italy: a new perspective for national conservation

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Abstract Loggerhead turtle *Caretta caretta* nesting in Italy had been reported to be limited to the Pelagian Islands and only sporadically elsewhere. As presence of loggerhead turtle nests had occasionally been reported (1988–1999) along about 200 km of the Ionian coast of Calabria, we carried out a project to assess the actual state of the nesting population between 2000 and 2004. We divided the coastline in two sectors (A: 52 km, and B: 146 km) that were monitored from mid-June to end of July for a total of $n = 174$ monitoring days and 1,813.6 km patrolled on foot with different intensities (extensive versus intensive). In sector B, through extensive monitoring we did not find any emergence tracks, but in sector A by intensive survey (2002–2004: one survey/3.64 days) we detected 3–8 nests/year. In total, 25 nests (both observed and reported), were recorded in our study area, and an assessment of a total of 15–16 nests/year was suggested. These figures, within the national scenario depicted from the review of known nesting events in the last 40 years (88 records concerning more than 143–144 nests), show that loggerhead turtle nesting has been underestimated in Italy, due to inadequate monitoring protocols, and that nesting is more frequent than expected (at least 30–40 nests/year). Conservation strategies in Italy should then focus not only on the reduction of mortality at sea, but also include large-scale actions to preserve scattered (but regular) nesting events.

Keywords Loggerhead turtle · *Caretta caretta* · Nesting distribution · Conservation · Italy · Mediterranean

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Introduction

The loggerhead turtle *Caretta caretta* is the most abundant sea turtle in the Mediterranean basin (Groombridge 1994). Despite its widespread distribution, nesting range extends almost exclusively to the Eastern Mediterranean. In a recent review, Margaritoulis et al. (2003) estimated at 5,031 the mean annual number of nests laid along the Mediterranean coasts, 60.6% ($n = 3,050$) in Greece, 27.1% ($n = 1,366$) in Turkey, 11.4% ($n = 571$) in Cyprus, and the remaining 0.9% ($n = 43$) in Israel and Tunisia. Moreover, Broderick et al. (2002), using data on clutch frequency and re-migration intervals from Cyprus, have calculated that the above annual number of nests corresponds to 2,280–2,787 females. These figures are minimum numbers (Margaritoulis et al. 2003) as they did not include data from sites other than monitored beaches or minor nesting aggregations known elsewhere (Egypt, Lebanon, Syria, Italy). Previous estimates have been recently corrected in some cases (e.g. in Turkey, where an average of 2,005 annual nests are estimated nowadays by Canbolat 2004). In addition, Laurent et al. (1995, 1997) have suggested the existence of a prominent population along the Libyan coast, but these preliminary results still need to be confirmed (Broderick et al. 2002; Margaritoulis et al. 2003).

As for spatial population structure, some authors (Bowen et al. 1993; Laurent et al. 1993, 1998; Schroth et al. 1996) detected significant genetic differences between the Mediterranean and Atlantic populations and, more interestingly, between Mediterranean sub-populations themselves, suggesting that Mediterranean rookeries are partially isolated from each other.

According to the IUCN “Red List” (Marine Turtle Specialist Group 1996), *C. caretta* is globally categorised as Endangered (criterion A1abd), and thus protected by international and European laws (Washington Conv., Appendix I CITES, All. II EC Dir. n. 206/22 1992, Appendix II Berne Conv.). The prolonged turtle trade, currently illegal but still lasting, the accidental catches, and the degradation of coastal and open sea habitats are the most probable causes of the increasing decline of the Mediterranean populations (Lutcavage et al. 1997; Tomas et al. 2002; Margaritoulis et al. 2003; Russo et al. 2003; Carreras et al. 2004; Casale et al. 2004; Lewison et al. 2004). Habitat degradation may have played a role by reducing hatchling recruitment, through the progressive destruction of nesting sites (human impact and coastal erosion), and increasing mortality at sea. Accidental catches, marine pollution, boat collisions and debris ingestion, among others, affect more than 35,000 turtles/year in the Mediterranean (Gerosa and Casale 1999).

Many local and international actions have been undertaken to reduce the declining process (e.g. Balletto et al. 2001a). Among conservation priorities, investigations of new nesting areas are recommended (PNUE-MAP 2000), as monitoring of the established nesting grounds is considered insufficient (Broderick et al. 2002).

Despite the lack of precise documentation (Groombridge 1994), *C. caretta* was thought to be regularly nesting along the coasts of southern Italy until the fifties. On the mainland, nesting events were recorded from Tuscany to Campania along the Tyrrhenian coast, and from Apulia to Calabria along the southern Adriatic and Ionian coasts; on islands, nesting grounds were known in Sardinia and in Sicily (Bruno 1986; Jesu 1995). First nesting confirmation was recorded in 1975 in Lampedusa (Pelagian Islands; Di Palma 1978), and a first survey to locate nesting areas was carried out in 1978 along several coastal sectors of southern Italy (Argano

and Baldari 1983). From 1981 to 1990, monitoring projects were pursued along extended coastal sectors, but only “*single nests*” were found (Cocco et al. 1988; Argano et al. 1992). However, detailed survey description or precise data on recorded nests appeared to be lacking (Groombridge 1994; Lescure 1997). Inadequate survey methodology could explain the paucity of results (Jesu 1995). At a smaller scale, some nests were located in Sicily (Di Palma et al. 1989), along the Ionian coast of Basilicata (Basso 1992, 1996), and above all in the two Pelagian Islands (Linosa and Lampedusa), where *C. caretta* nesting is at present more regularly monitored (Gramentz 1986; Di Palma et al. 1989; Freggi 1997; Dominici et al. 2000; Bombace et al. 2001; Piovano et al. in press).

Loggerhead turtle nesting in Italy was therefore stated to be an “*occasional and sporadic event*” (Argano et al. 1991; Jesu 1995), or also “*virtually ceased*” (Argano and Cocco 1988 in Groombridge 1994), except for the Pelagian Islands, which were reported to be the last documented and certain nesting site still present in Italy (Balletto et al. 2001b). According to this, an EU Life-Nature project was carried out in 1999 (Giacoma and Solinas 2001). Finally, Margaritoulis et al. (2003) estimated at 15 the maximum annual number of nests in the country.

Nevertheless, ten nests were documented along the Ionian coast of Calabria from 1988 to 1999 (Paolillo et al. 2000). As all the nests were accidentally discovered by tourists and none through monitoring (in opposition to what stated by Gerosa et al. 1999, 2000), and no real field surveys have ever been conducted along the hundreds of km of this coastline, nesting is likely to have occurred undetected at higher frequencies than reported (Mingozzi et al. 2000). Consequently, in spring 2000 a project to assess the magnitude of nesting activity along the Ionian coast of Calabria was carried out (Mingozzi et al. 2004).

The aim of this paper is to present the results of our 5-year study (2000–2004). We provide an overview of nesting of loggerhead turtle in Italy in the last 40 years to frame the relevance of our results in the national scenario. We then evaluate the efficacy of the current survey methods of loggerhead turtle nests when applied over long coastlines. Finally, we propose a new perspective in conservation of loggerhead turtles in Italy.

Methods

Study area

The study area is located along the Ionian coast of Calabria, the southernmost part of the Italian peninsula (Fig. 1). The coastline extends from Crotone southward about 245 km to Reggio di Calabria, facing the Messina Straits. The survey was performed along the coastline between Le Castella ($15^{\circ}40'00''E$, $37^{\circ}57'17''N$) and Capo dell’Armi ($15^{\circ}40'50''E$, $37^{\circ}57'12''N$), for an extension of 198.1 km, 11.8% ($n = 23.4$ km) represented by rocky cliffs or highly eroded coast, the rest (88.2%, $n = 174.8$ km) being low-lying sandy (or sandy-shingly) beaches (potential nesting coastline), wider than 50 m for about 50 km (28.6%), the rest being narrower.

Beach monitoring

The study was carried out across five seasons (2000–2004). In accordance with the peak of temporal nesting distribution observed on Greek beaches (Margaritoulis

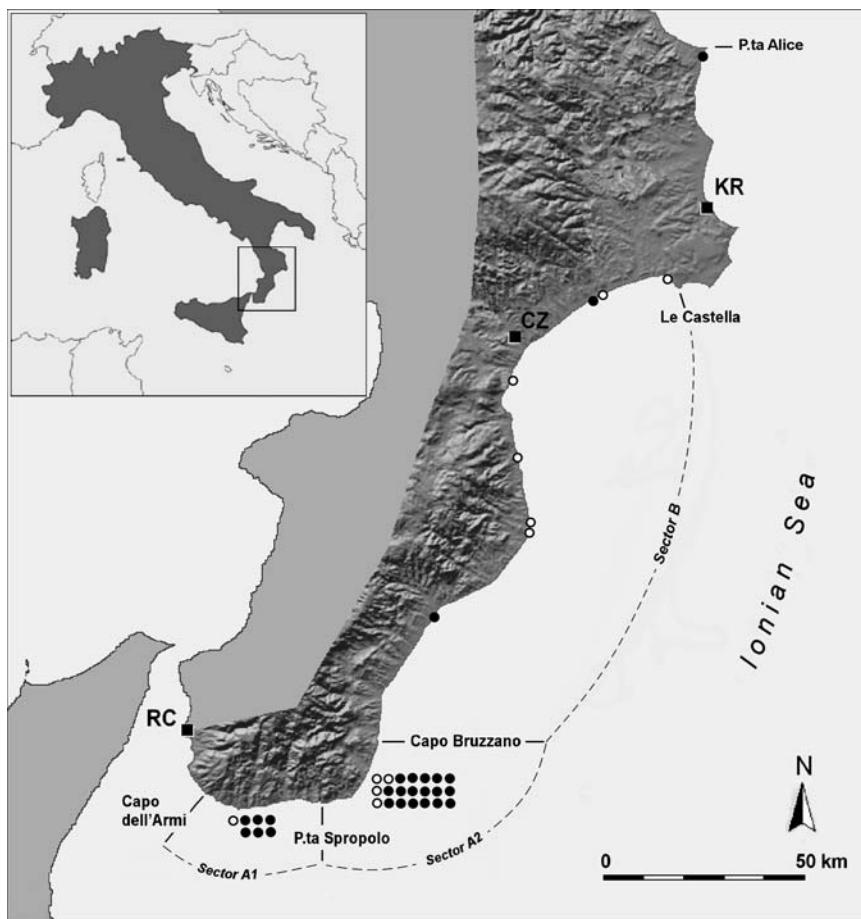


Fig. 1 Nest distribution of loggerhead turtle along the Ionian coast of Calabria from 1988 to 2004. White dots: nests recorded from 1988 to 1999. Black dots: nests recorded during the monitoring project 2000–2004. Dashed line shows the priority sector A (A1, from Capo dell'Armi to P.ta Spropolo; A2 from P.ta Spropolo to Capo Bruzzano) and the secondary sector B (from Capo Bruzzano to Le Castella). Main towns: Reggio Calabria (RC); Catanzaro (CZ) and Crotone (KR)

1988), our monitoring programme ran from mid-June (except in 2000 at the end of June) to around 20 July (except in 2004 at the end), but the number of monitoring days varied from 17 (2000) to 49 (2004), with a mean of 34.8 days/season \pm 4.8 (SEM), for a total effort of 174 days in five seasons (Table 1).

From 2000 to 2004, 77.1% ($n = 135$ km) of the potential nesting coastline (175 km), was patrolled at least once, and the number of monitored km per year varied from 48 (2000) to 97 (2001), with a mean of 65.8 ± 7.4 km. The monitoring effort increased regularly from 163.4 (2000) to 526.8 km (2004) patrolled, with a mean of 362.7 ± 61.1 km, on the whole $n = 1,813.6$ km.

We defined two sectors along the coastline (Fig. 1): sector A (southern sector), 52 km from Capo dell'Armi to Capo Bruzzano ($16^{\circ}08'38''E$, $38^{\circ}01'52''N$); sector B (northern sector), 146 km from Capo Bruzzano to Le Castella. Sector A had 40 km

Table 1 General results of the 5-year (2000–2004) survey of loggerhead turtle nesting along the Ionian coast of Calabria (southern Italy)

| | Years | | | | |
|-----------------------------------------------------------|---------|---------|---------|---------|---------|
| | 2000 | 2001 | 2002 | 2003 | 2004 |
| Survey starting | 27 June | 5 June | 11 June | 16 June | 12 June |
| Survey ending | 23 July | 22 July | 21 July | 20 July | 31 July |
| Monitoring days (total $n = 174$) | 17 | 42 | 33 | 33 | 49 |
| Monitored beach length (km) (total $n = 135$) | 48 | 97 | 65 | 62 | 57 |
| Cumulative patrolled kilometre (total $n = 1813.6$ km) | 163.4 | 281.7 | 339.2 | 502.5 | 526.8 |

The table reports the monitoring period for each year (starting and ending date), the total number of monitoring days/year, the extent of monitored beach length (km), and the annual monitoring effort calculated as the cumulative kilometre patrolled

(76.9%) of Potentially Suitable for loggerhead turtle Nesting coastline (PSN from now on), while sector B had 135 km PSN coastline (92.5%).

We adopted two monitoring approaches, “extensive” and “intensive” during the project in the two sectors (Table 2). In its preliminary phase (2000–2001) the survey was carried out extensively along 99 of 175 km (56.6%) of coastline. Mean survey interval was of 7.8 days (i.e. a monitoring frequency of one survey each 7.8 days).

In the second period (intensive phase, 2002–2004), our monitoring effort was focused on sector A, where most of the nesting evidences had been found in the previous years, whilst sector B was monitored at lower frequency (about one survey/14 days). Furthermore, sector A was divided in two sub-sectors: A1 (35.5 km), from Capo dell’Armi to Punta Spropolo ($16^{\circ}02'46''$ E, $37^{\circ}55'18''$ N); A2 (16.5 km), from Punta Spropolo to Capo Bruzzano. Then, the monitoring effort in these two sub-sectors was stratified (A1: one survey/4.2 days; A2: one survey/3.1 days) on the basis of the previous results.

Every season, the beaches were patrolled on foot by two or three teams of two–three observers for turtle emergences (i.e. non-nesting or nesting tracks (Nt), see

Table 2 Results of the sampling effort (ground patrols on foot) along the two sectors A and B (PSN, Potentially Suitable for Nesting), during the preliminary (2000–2001) and core (2002–2004) periods of the monitoring project of loggerhead turtle nesting along the Ionian coast of Calabria (southern Italy)

| | Sector A (PSN: 40 km) | | Sector B (PSN: 135 km) | |
|---------------------------------------------------------------------|-----------------------|-------------|------------------------|--------------|
| | 2000–2001 | 2002–2004 | 2000–2001 | 2002–2004 |
| Monitored beach length (km) | 20 | 40 | 79 | 39 |
| Cumulative patrolled kilometre | 208 | 1540 | 306 | 145 |
| n surveys/km (cumulative patrolled km/monitored beach length, km) | 10.4 | 34.2 | 3.9 | 3.7 |
| Mean monitoring interval (days) between successive surveys (SEM) | 7.13 (0.51) | 3.64 (0.14) | 8.40 (0.92) | 14.54 (2.24) |
| Turtle emergences directly observed | 3 | 38 | 0 | 0 |

The table reports the length of monitored coastline (km), the cumulative patrolled coastal extension (km), the number of surveys per km, the mean time interval in days (SEM) between successive surveys, and the total number of turtle emergences directly observed per sector and period by our team

below). For the purpose of the survey, sector A was divided into 12 “routes” (beaches) of variable length (range: 560–7,780 m), likewise sector B was divided into 21 routes (range: 500–7,200 m). Usually, the teams worked together to patrol contiguous routes so that the second team began their survey where the first team terminated.

The patrols were usually done early in the morning (6.00–9.00 a.m.) and late in the afternoon (5.00–8.00 p.m.), to take advantage of the most favourable light conditions and of the lower temperatures. Tracks were obliterated after all data had been recorded (see below) to avoid recounting the same tracks on subsequent survey.

Given the large extension of potentially suitable coastline, we did not try to locate nesting females during emergence, so patrols at night were never performed.

Nest monitoring

We did not dig any potential nest. We used only track morphology to establish whether a clutch had been laid or not. We adopted the Laurent et al. (1995) classification of emergence tracks as: (a) visiting tracks (V_t), tracks without any digging attempt; (b) digging tracks (D_t), track with one or more digging attempts but no egg deposition and (c) N_t , track where digging and covering have occurred and egg laying is likely. Emergence tracks identification was verified later in the season, as were suspected nesting tracks which were checked for laid nests that did not hatch (see below).

All tracks were marked on a 1/25,000 national map and since 2003 have also been georeferenced by means of a hand-held GPS (GPSmap 60CS, Garmin®, UK). Potential nests were also tagged by ground markers to allow for successive re-location. Nests at risk of being damaged by human activities were protected with a wooden fence. Track characteristics (length, width, distance to dune, etc.) as well as nest characteristics (minimum and maximum nest chamber depth) were recorded after hatchling emergence.

To assess hatching date, an incubation duration (i.e. number of days elapsed from egg-laying to the emergence of the first hatchling. Margaritoulis 2005), of 45–70 days was assumed (Margaritoulis et al. 2003). During this “hatching period”, each potential nest was checked from sunset to midnight or at dawn for signs of hatchling emergence as indicated by tracks on the periodically smoothed area.

Hatched nests were excavated 7–14 days after hatchling emergence (Margaritoulis 1988) to calculate clutch size (n of laid eggs) and hatching emergence success (i.e. n of hatched eggs/ n of laid eggs). Unhatched nests were excavated at the end of the season (end of September).

National nesting overview

To frame our results in the national scenario, all the available nesting events recorded in Italy since the 1960s were collected (see Table 3), through a review of the published literature, symposia and congresses proceedings, but also of national and local daily newspapers, and by direct interview to research and conservation workers (see acknowledgements).

In many cases, available nesting data (published or not) were lacking in precision and details. Thus, special attention was paid to assess data reliability (not possible for historical records), and in the present list data validation was obtained by cross-controls to verify: (a) the geographical location: for each record, original locality

references were checked and, if needed, complementary place names were quoted in italic (i.e. municipality and/or place name next to the beach); whenever place name could not be specified, notation *locus incognitus* (*loc. inc.*) was given. (b) The reference date: the most probable year was assumed whenever references were not agreeing for the same record. Simple emergence tracks were not quoted as nesting data. For each record, only the main references are reported (the original, and if needed, a supplementary one).

On the whole, our conservative validation method brought to exclude various previous reports, above all for Sicily where historical records have shown the greatest uncertainty.

Statistical methods

We compared occurrence of emergence tracks in different coastal sectors by means of Pearson Chi-squared, while we used Spearman correlation analysis to test for independence of monitoring effort and recorded emergence tracks in sub-sectors A1 and A2 (Siegel and Castellan 1988; Sokal and Rohlf 1995). After reclassification of the monitoring time intervals into two classes (1, ≤ 4.5 days; 2, >4.5 days), we used the Pearson Chi-squared to test track occurrence in the two sub-sectors of sector A (A1 and A2) monitored with different frequency (different time interval classes).

The probability levels were computed using a complete randomisation method (permutation or exact test; P_{Exact}), or by a Monte-Carlo simulation based on a 10.000 sampled tables ($P_{\text{Monte-Carlo}}$) when computation was not possible (Mehta and Patel 1996; Good 2000).

Statistical analyses have been carried out using SPSS 12.01 (Statistical Package for Social Sciences, [®]SPSS Inc., Chicago, IL, USA).

Results

Nest number and distribution

An overview map of the nests located ($n = 36$) in the study area from 1988 to 2004 is shown in Fig. 1. Apart from the ten nests recorded between 1988 and 1999 (Paolillo et al. 2000), and one more nest documented afterwards for the same period, 25 nests were recorded in our study area during the research project 2000–2004. One additional nest was documented 48 km north of the study area in 2003 (Cirò Marina, next to Punta Alice, Fig. 1). In the study, area 17 nests (68.0%) were discovered during the monitoring programme, while the rest have been accidentally found by tourists or local people (cf. Table 3). Most of 2000–2004 nests ($n = 23$, 92.0%) were concentrated in sector A, and, in particular, in sub-sector A2 ($n = 17$), the so-called “Costa dei Gelsomini”, where four (36.4%) of previous nests (1988–1999) were located. All 17 nests of the sub-sector A2 were found by our team during the intensive study period (2002–2004) (range = 3–8 nests/year). Only two nests were documented in sector B (where six resulted in 1988–1999).

Monitoring efficiency

Through the extensive monitoring performed during the preliminary phase (2000–2001), we did not find any track in sector B, and only three (one Vt and two Dt) in

sector A (Table 2). Pooling directly observed records ($n = 3$) with reported ones (*ex alii*, $n = 9$), turtle emergences were clearly more frequent in sector A ($n = 12$) than in sector B ($n = 1$), as comparable monitoring effort (one survey/7.13 days and one survey/8.40 days, respectively) was spent, and sector B has a much greater extension of PSN coastline (135 km vs. 40 km).

From 2002 to 2004, the intensive survey in sector A showed a greater nesting activity than in the previous period (12.7 tracks/year vs. 1.5 tracks/year), possibly as a consequence of a more intensive monitoring (mean interval, 3.64 days vs. 7.13 days; Table 2), although the effect of natural annual fluctuations cannot be excluded. Direct observations of emergence tracks ($n = 38$, 92.7%) were more frequent than reported ones (*ex alii*, $n = 3$, 7.3%).

In sector A, pooling the data collected during the monitoring programme for the whole study period (2000–2004), track occurrence seemed to be significantly associated with the time elapsed between successive surveys ($\chi^2 = 5.932$, $df = 2$, $P_{\text{Exact}} = 0.050$).

Furthermore, in sector A monitoring effort seemed adequate to detect all nesting events (Fig. 2), as we found no association between monitoring effort and emergence tracks density in both A1 and A2 sub-sectors from 2002 to 2004 ($r_s = -0.113$, $P = 0.090$ and $r_s = -0.007$, $P = 0.913$, respectively).

Reproductive parameters

On a weekly basis, 23.7% ($n = 12$) of nesting emergences from 2000 to 2004 for which dates were known ($n = 44$) appeared to peak between 4th and 10th July (in

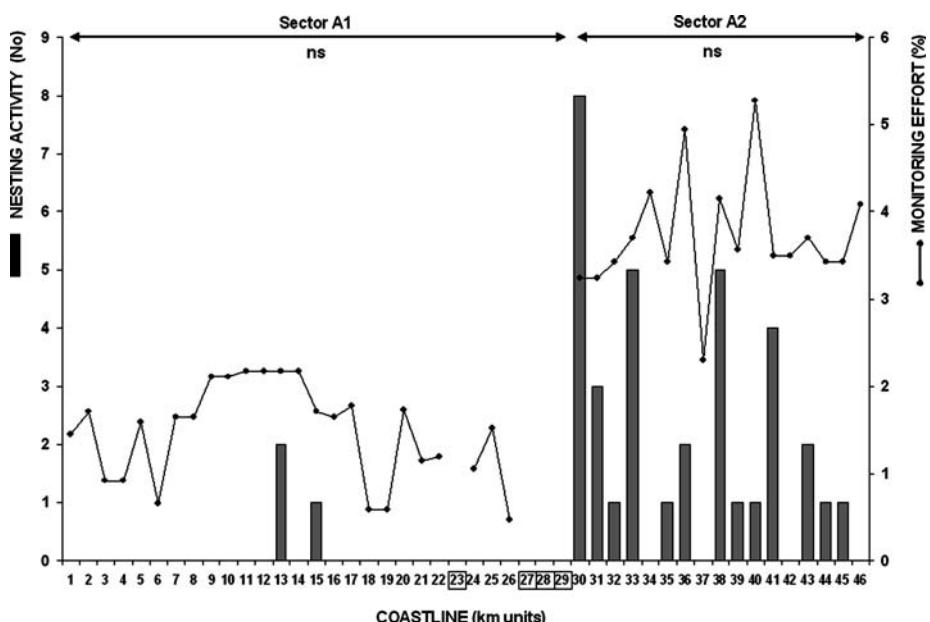


Fig. 2 Nesting activity (nests or not-nest tracks, $n = 38$, grey bars) of loggerhead turtle recorded along 46 of 52 km of the priority sectors A of the Ionian coast of Calabria in 2002–2004, monitored with different intensity (black line) in sectors A1 versus A2. The figure reports the results of Pearson correlation analysis between monitoring effort and recorded number of nesting events. ns not significant. Kilometre sectors entirely eroded are highlighted with boxes (six more, eroded or anyway unsuitable, are not included in the figure)

Greece, the modal class was a week later; Margaritoulis 1988). In average, incubation duration (three seasons, $n = 11$) lasted 45.6 ± 1.6 days (range = 36–53). Notably, the minimum verified duration (36 days) has never been previously recorded for this species. During the whole study period, we checked the success of 17 nests: four were destroyed before hatching (two by sea storm and inundation, one by cars, one by unknown causes), and 13 hatched successfully. The all-years mean clutch size was of 99.0 ± 5.85 eggs (range = 50–134), with an all-years mean hatching emergence success of $86.0 \pm 4.0\%$, and a total estimate of about 1,300 hatchlings released. From 2002 to 2004, the mean seasonal nesting success (laid nests over emergence tracks) was $43.6 \pm 0.97\%$ ($n_{Vt} = 5$, $n_{Dt} = 17$ and $n_{Nt} = 17$). No statistical difference in nesting success was detected between the 2000–2001 and 2002–2004 seasonal surveys in sector A ($\chi^2 = 0.152$, $df = 1$, $P_{Exact} = 0.749$).

National nesting overview

We collected 88 records concerning more than 143–144 nests recorded in Italy (Mainland $n > 51$; Islands $n = 92$ –93) in 40 years (1965–2004; Table 3). Most of the records (80.7%, $n = 71$) referred to nests discovered from 1985 to 2004, and many of them (38.0%, $n = 27$) were unpublished.

Figure 3 shows a former nesting distribution (1965–1999) spread along most of southern Italian coasts, above all (91.9%, $n = 57$ records) along its south-eastern side (southern Adriatic Sea, Ionian Sea and Sicilian Channel), while sporadic records (8.1%, $n = 5$) were documented elsewhere (Tyrrhenian Sea).

In particular, from 1985 to 1999 nesting was confirmed ($n = 74$ –75 nests) in four main sectors: the Ionian Sea coastline, from Apulia to Calabria (27.0%, $n = 20$); the southern Sicilian coast (20.3%, $n = 15$); the Pelagian Islands (50.0%, $n = 37$ –38); the southern and western coast of Sardinia (2.7%, $n = 2$). At a national scale, peaks in nests number were reached in 1994 (17 nests at least) and in 1996 (10 nests).

The current distribution pattern (2000–2004), coming out from an highly heterogeneous degree of coastline investigation, confirmed the same four nesting areas, although reduced in range: the Ionian coast of Calabria (southern sector A: monitored; northern sector B: insufficiently monitored); the central sector of the southern Sicilian coast (not monitored, except for a very few and short beaches; F. Galia and G. Insacco, personal communication; Piovano et al., in press); the Pelagian Islands (monitored), where nesting was regularly confirmed, although not annually; the south-western coast of Sardinia (the “Costa Verde”), insufficiently monitored.

Moreover, the unprecedented nesting event of 2002 in Baia Domizia (Tyrrhenian Sea, Campania) (Centro Studi Cetacei 2002) needs to be added as the northernmost documented evidence ($41^{\circ}10'N$) recorded up to now in Italy, a few degrees south of the northernmost recorded nesting locality in the Mediterranean (Palombaggia beach, Corsica, Delaguerre and Cesarini 2004; $41^{\circ}33'N$).

On a quantitative point of view, the national overview revealed that the Ionian coast of Calabria (southern plus northern sector) reached 52.0% ($n = 26$) of the total nesting events documented within Italian political borders ($n = 50$), and 83.9% of nesting records ($n = 31$) within Italian biogeographical borders, if the Pelagian Islands (and particularly Lampedusa, not volcanic) are correctly considered part of the African continent (Agnesi and Federico 1995).

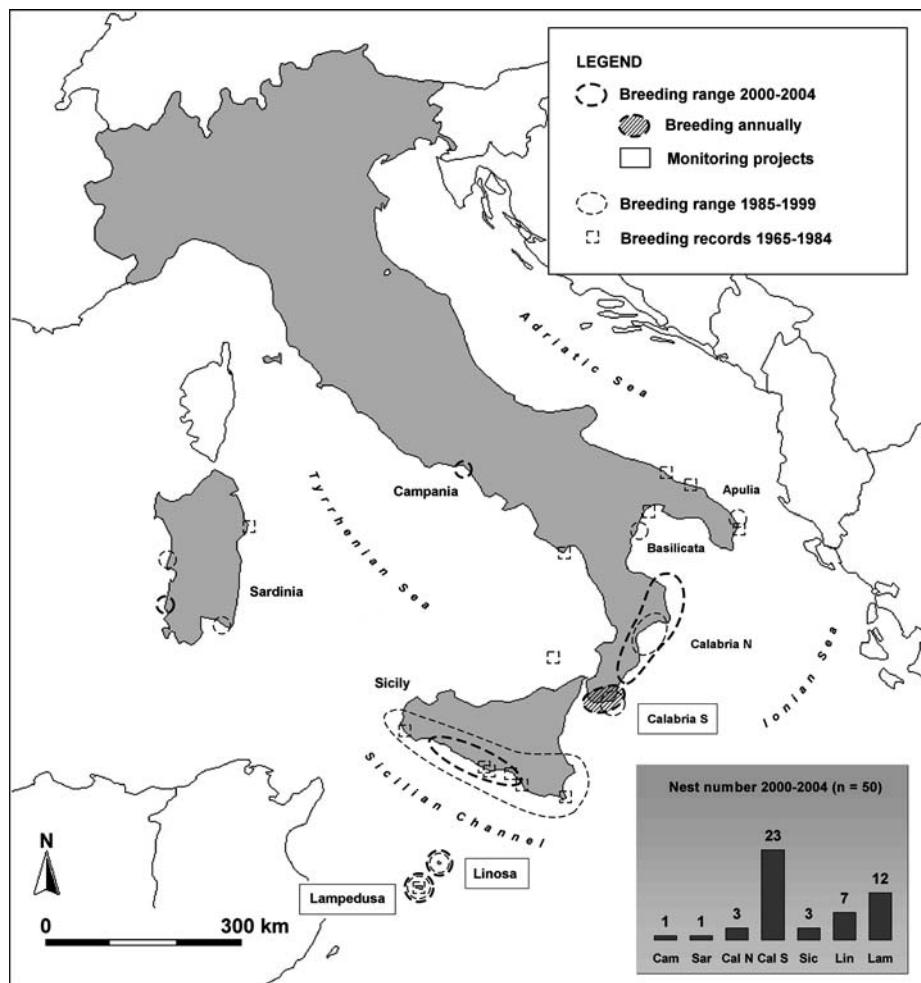


Fig. 3 Nesting distribution of loggerhead turtle in Italy during the last 40 years (1965–2004). Data were clustered in three main periods: (a) nests recorded in the last 5 years (breeding range 2000–2004); (b) nests recorded in the previous 15 years (breeding range 1985–1999); (c) nests recorded during the first 20 years (breeding records 1965–1984). Current breeding range (2000–2004) is differently marked whereas nesting evidences were annually recorded, and if data were due to intense monitoring projects. Number of nests in the areas concerned is highlighted in the lower right (see Table 3 for references and details)

Finally, the southern coast of the Ionian Calabria (sector A) resulted at present to be the only national area where *C. caretta* nesting has been recorded annually.

Discussion

Nesting in the Ionian coast of Calabria

Our data clearly show the existence of a regular nesting area along the Ionian coast of Calabria, a totally unexpected finding according to the literature. As a matter of

fact, since the beginning of this study (2000) emergence tracks were annually found along this coastline, in particular in the southern sector A where our monitoring programme was mostly concentrated. Notably, the ten nests which were occasionally found in decade prior to our study (1990–1999), were equally distributed in sector A and in sector B, with $n = 5$ nests each, thus suggesting a differential nesting activity in these two sectors, as B is nearly three times larger than A.

Our data (2002–2004) suggest that an average of 5.67 ± 1.19 nests (range = 3–8) were annually laid in sector A, but this is a figure that is likely to be increased. In fact, we possibly missed some nests as our monitoring period focused on the core nesting period of this species (Table 1), and not on its entire nesting season (which in the Mediterranean basin varies between colonies, but it extends for nearly three months; e.g., Greece, Margaritoulis 2005; Turkey, Erk'akan 1993; Cyprus, Broderick et al. 2002). Actually, some later emergences have been occasionally found (28 August 2002), and some early nesting cannot be excluded, as suggested by the incoming results of the monitoring season 2005 (first emergence on 6th June).

Furthermore, if knowledge about inter-nesting interval and site fidelity (Broderick et al. 2002; Schroeder et al. 2003) is applicable on our study area, we may have missed some nests, as in some cases emergence tracks were not clearly followed by nesting evidences.

Following these considerations, we may conservatively estimate that at least two nests were missed each year in sector A (one before and one after our monitoring season); hence, 7.67 ± 1.19 nests/year (range = 5–10) may be estimated.

The absence of data for the northern sector B depended likely on the monitoring schedule, that was not feasible for such an extent of coastline. An adequate nesting survey along 135 km of potentially suitable coastline would have been difficult to perform due to personnel and equipment costs beyond the available budget. Nonetheless, as nests were occasionally found by tourists along the whole coast, it is likely that other nesting areas were present. In fact, the occasional findings in 1999 were all referable to beaches where tourist density was very high in August (Russo 2001), and no nests were documented elsewhere.

These results stress that historical and recent data (before 2000) of loggerhead turtle nests found along the Ionian coast of Calabria were an underestimate of the actual phenomenon, that is regular and relatively substantial (according to local witnesses, nesting was widespread in the past, as until the last post-war period egg harvesting for food was a usual activity for local inhabitants; L. Gatti personal communication).

The relatively low density of nesting, if compared to eastern Mediterranean colonies, along with the large extension of beaches that are potentially suitable for nesting (175 km only in our study area), are both crucial factors that may have conditioned the correct quantitative assessment of nesting. Moreover, emergence tracks did not last for more than a few days (in agreement with Laurent et al. 1995), particularly in case of adverse weather conditions (rain, wind or rough sea) or intense human presence.

Hence, to correctly survey loggerhead turtle nesting in such conditions, monitoring should be conducted with higher frequency than once or twice a season (no more than a 4-day interval between successive surveys; e.g. Clarke et al. 2000) which may have brought, not only in our study area, to a great data loss.

Similar problems of nesting survey over large extensions in the Mediterranean Sea were probably common to Kasparek (1991) in the northern Aegean Sea, to

Laurent et al. (1995, 1997) in Libya, to Clarke et al. (2000) in Egypt, and to Kuller (1999) in Israel, whose estimates are possibly conditioned (underestimated) by the low frequency of patrols per beach along great coastline extension (i.e. 664 km in northern Aegean Sea, 1,144 km in Libya, 616.5 km in Egypt and 190 km in Israel).

We suggest that, in case of large extensions, terrestrial patrols should be complemented, if not replaced, by aerial patrols as already experimented elsewhere: by plane (Crouse 1984 in North Carolina; Carr and Carr 1991 in Angola; Epperly et al. 1995 in North Carolina), by helicopter (Garmestani et al. 2001 in Florida), or by motor-assisted delta-plane (micro-light) (Barazzutti in Congo; Billes 2000).

During the first year of our study (2000), an attempt of aerial survey was carried out by two of us (TM and MR) using a motor-assisted delta-plane conducted by a pilot. In 5 days (27 June–2nd July) an extension of 87.7 km of coastline was surveyed for a total of 335.2 km (flying time: 6 h: 43'), at an average speed of 50 km/h, and at a flight altitude of about 40–50 m. This monitoring method was then abandoned due to the high-running costs, and to the risks connected to the lack of safe runways and landing strips. The use of off-roads vehicles was excluded for their impact on the habitat. Hence, we are planning to experiment the use of modified micro-light supplied with an inflatable boat (Flying Inflatable Boat, FIB), which may reduce risks and is not limited by availability of landing strips.

Local and national overview

The number of nests found during the three seasons of intense monitoring (2002–2004) exceeded our expectations, as the annual nesting occurrence along sector A (3–8/year, but four to ten nests along the entire study area) was greater than reported for the Pelagian Islands, the only other Italian areas submitted to regular surveys (pooled data for the Pelagian Islands, 0–8/year), but where nesting was confined to very small beaches as Conigli beach (400 m long and 30 m wide), and Pozzolana Beach (100 m long, 7 m wide; Di Palma et al. 1989).

If we use the estimated average of nests/year ($n = 7.67$) from sector A, and the ratio between the occurrence of reported records 1990–1999 in sector B to those in sector A (1:1 ratio), to assess the nesting population along the entire coastline of Ionian Calabria (sectors A + B, 135 km), then we would expect about 15–16 nests/year.

Although these figures are probably underestimates of the actual situation they are quite impressive if compared with data from other Italian nesting areas (Fig. 3). As stated above, it is likely that the intensity of loggerhead turtle nesting has been underestimated elsewhere in Italy, particularly in Sicily, but also on the Mainland (southern Adriatic–northern Ionian coasts), and Sardinia. The southern coast of Sicily is characterised by long beaches that were not (with some exception) regularly and/or intensively monitored, and it is likely that many nests went undiscovered. Currently, any estimate of the Sicilian nesting population would be speculative at best.

Nonetheless, considering that there are at least 441 km of total coastline extension in southern Italy (i.e. 281 km in the Ionian Calabria and 160 km in Sicily) where loggerhead turtle nesting is actually occurring (plus Pelagian Islands, and other more documented nesting areas), the recent estimate of 15 nests/year of Margaritoulis et al. (2003) is certainly too conservative. We estimate that at least 30–40 nests are annually laid in Italy, and that the Ionian coast of Calabria may host a portion of the

whole Italian nesting population that is certainly relevant (52%), but probably lower than shown by our current data.

On the whole, three main types of nesting areas could be currently recognised in Italy: (a) regular and annually nesting areas (southern coast of Ionian Calabria); (b) regular, but not annually, nesting areas (Pelagian Islands); (c) occasional nesting areas (southern Tyrrhenian coasts of mainland). On the basis of the current knowledge, the northern coast of Ionian Calabria, and the southern coast of Sicily may belong to (a) or (b) class at least, whereas any classification for nesting areas documented elsewhere (Sardinia, Basilicata and Apulia) would be insubstantial.

Conservation status of the Calabrian population

From 2002 to 2004, the mean annual nesting success (43.6%), was comparable to those reported for the Greek colonies (Margaritoulis 1988; Margaritoulis et al. 2003), the mean hatching emergence success was much higher (86.0% vs. 55.6%), although recent data reported higher values (71.5%; Margaritoulis 2005), and the mean clutch size was lower (99.0 eggs vs. 117 eggs; Margaritoulis 2005).

Despite these favourable figures, the Calabrian nesting population is seriously endangered not only by high-mortality rates at sea (accidental catches by trawling and hooks, craft collisions, debris ingestion; Paolillo et al. 2000; Pisani 2002), but also by direct threats during the deposition, incubation and hatching phases. The impact of off-road vehicles, beach cleaning or mechanical levelling in the summer and the increase of artificial lights are likely to be the major causes of nesting failure, despite a relative low level of coastal exploitation (30% of urbanisation and 50% of beaches interested by important tourist activity in sector A; Russo 2001). Conversely, nest predation (one of the most important causes of nesting failure at many Mediterranean nesting grounds; Margaritoulis et al. 2003), was never documented in Calabria.

Finally, habitat loss due to coastal erosion may have played a crucial role in decreasing nesting success. As a matter of fact these processes, that affect about 56.6% (112 km) of the whole study area (D'Alessandro et al. 1993) are likely to have already cut off quite a few kilometres of potentially suitable coastline in southern sector A.

Conclusions and the new conservation perspective

The state of loggerhead turtle nesting in Italy is far from clear, although our data suggest that the phenomenon is likely to be greater than expected. As strongly suggested by Seminoff (2004), a survey campaign to asses regional nesting populations is now most needed, particularly in those areas where nesting was documented in the past 10 years. The Ionian coast of Calabria, and in particular its southern sector, should then be reconsidered relevant for national conservation due to its substantial and regular contribution to the nesting pool. Analogously, the Sicilian scenario is probably underestimated. We strongly recommend a re-evaluation of the Italian perspective to identify and mitigate threats to loggerhead turtles that are nesting in these areas.

Despite the small number of nesting females, derived from the small number of nests, the increasing knowledge on the processes of genetic diversification of

neighbouring colonies (Schroth et al. 1996; Laurent et al. 1998; Plotkin and Spotila 2002) should focus the conservationists attention on the protection of small rookeries, that may play an important role in maintenance of genetic diversity. Quoting Schroth et al. (1996), the natal homing behaviour of the females “*makes it unlikely that the loss of nesting habitat [...] can be compensated for by emigration to other colonies; that is the loss of nesting sites is accompanied by the loss of specific genotypes*”. Consequently, the protection of nesting sites should be increased to reduce habitat loss (Clarke et al. 2000), hence preserving genetically unique nesting sites.

Despite the obvious conservation value of protection of nesting sites, other relevant outputs in terms of economic and social re-qualification of the areas being protected are expected. The hypothesis of creating a sort of “Marine turtle coast” in southern coast of Ionian Calabria would certainly improve the tourism industry, thus contributing to local economy.

Unfortunately, to obtain such results we should change the traditional national approach to conservation of marine turtles. By now, national/local conservation strategies in some countries are focused mostly on the reduction of mortality in the pelagic phase (e.g. Balazs and Chaloupka 2004; Casale et al. 2004), and only on the protection of nesting sites that are easy and cheap to protect (i.e. in Italy, the small beaches of the Pelagian Islands). This is possibly due to the lack of important nesting beaches that directs conservation efforts towards the sea where incidental catch by trawls and long-lines is great (e.g. Deflorio et al. 2005).

Obviously, conservation should try to protect the maximum with the minimum effort (Mast 1999), but whenever this is not possible, alternative strategies should be undertaken. We strongly suggest the introduction of a large-scale conservation approach that not only aims at reducing pelagic mortality, but also protects the most likely nesting areas (Calabria and Sicily).

This strategy should include a preliminary phase to precisely assess the local nesting distribution over large coastline extensions through intense monitoring (three-day intervals between successive patrols, along a sample of beaches), and then should implement short-term actions focused on the protection of nests, and by medium- and long-term actions to reduce uncontrolled urbanisation (buildings, artificial lights, etc.), coastal erosion and/or beach nourishments (Rumboldt et al. 2001).

Table 3 Nests of loggerhead turtle identified in Italy from 1965 to 2004 (minimum $n = 143$ –144)

| | Year | Nests n | Locality | Lat N | Long E | Sea | References |
|--------------------------|---------------|---------------------------------------|----------------------------------------------------------|------------------------|------------------------|---------------------------------------------------------|----------------------------------------------------------------------|
| <i>Mainland (n = 51)</i> | | | | | | | |
| Apulian (n = 7) | Before 1973 | 1 | Monopoli <i>Castellana Marina</i> , Torre del Lato | 40°57'29" 40°28'13" | 17°18'19" 16°56'44" | Adriatic Ionian | Pozio and Frisenda (1977) Pozio and Frisenda (1977) |
| | Before 1973 | 1 | Carovigno, <i>Torre S. Sabina</i> (?) | 40°45'34" | 17°42'14" | Adriatic | Pozio and Frisenda (1977) |
| | Before 1973 | 1 | Otranto, Capo d'Oronto | 40°06'28" | 18°31'12" | Adriatic | Pozio and Frisenda (1977) |
| | 1994 | 3* | Otranto, Laghi Alimini | 40°11'32" | 18°28'15" | Adriatic | Basso (1996) |
| Basilicata (n = 6) | 1988 | 1 | Policoro, Foce Sinni | 40°11'31" | 16°43'15" | Ionian | Basso (1992) |
| | ? (1989–1990) | 1 | Scanzano Ionico | 40°13'36" | 16°44'44" | Ionian | Basso (1996) and ARCA and R. Basso (personal communication) |
| | 1991–1994 | 4* | Scanzano Ionico | 40°13'36" | 16°44'44" | Ionian | Basso (1996) and ARCA and R. Basso (personal communication) |
| Calabria (n = 37) | 1988 | 1 | Stalettì, Pietragrande | 38°45'59" | 16°32'18" | Ionian | Basso (1992) and Russo (2001) |
| | 1991 | 1 | Isca sullo Ionio | 38°36'08" | 16°31'13" | Ionian | Paolillo et al. (2000) and Russo (2001) |
| | 1992 | 1 | Sellia Marina | 38°53'13" | 16°45'00" | Ionian | Paolillo et al. (2000) and Russo (2001) |
| | 1992 | 1 | Monasterace | 38°27'16" | 16°33'10" | Ionian | Paolillo et al. (2000) and Russo (2001) |
| | 1994 | 1 | Palizzi Marina | 37°58'03" | 15°59'15" | Ionian | Paolillo et al. (2000) and Russo (2001) |
| | 1994 | 1 | Monasterace | 38°27'16" | 16°33'10" | Ionian | Paolillo et al. (2000) and Russo (2001) |
| | 1997 | 1 | Brancalone | 37°55'53" | 16°41'20" | Ionian | Present research (<i>ex auct.</i>) |
| | 1998 | 1 | Cutro, Praialonga | 39°02'10" | 16°38'57" | Ionian | Paolillo et al. (2000) and Russo (2001) |
| | 1999 | 1 | Marina di San Lorenzo | 37°55'22" | 15°49'59" | Ionian | Paolillo and Florio (2000), Gerosa et al. (1999) and Russo (2001) |
| | 1999 | 2 | Brancalone | 37°55'53" | 16°41'20" | Ionian | Paolillo and Florio (2000), Gerosa et al. (1999) and Russo (2001) |
| | 2000 | 1* | Simeri Crichi | 38°52'33" | 16°43'31" | Ionian | Present research (<i>ex auct.</i>) |
| 2000 | 2* | Palizzi Marina | 37°58'03" | 15°59'15" | Ionian | Present research (G. Tuscano personal communication) | |
| 2001 | 1* | Melito Porto Salvo, Capo dell'Armi | 37°57'14" | 15°40'49" | Ionian | Present research (<i>ex auct.</i>) | |
| 2001 | 1* | Marina di San Lorenzo | 37°55'22" | 15°49'59" | Ionian | Present research (<i>ex auct.</i>) | |

Table 3 continued

| | Year | Nests n | Locality | Lat N | Long E | Sea | References |
|---------------------------------------------|-------------|-----------------------------------|-------------------------------------|------------|------------|--------------------------------------|-------------------------------------------------------|
| | 2001 | 2* | Palizzi Marina | 37°58'03" | 15°59'15" | Ionian | Present research (S. Stranges personal communication) |
| 2002 | 3* | Bruzzano, Ferruzzano | 38°00'59" | 16°08'16" | Ionian | Present research | |
| 2003 | 1* | Bruzzano, Ferruzzano | 38°00'59" | 16°08'16" | Ionian | Present research | |
| 2003 | 4* | Brancalone | 37°55'53" | 16°41'20" | Ionian | Present research | |
| 2003 | 2* | Palizzi Marina | 37°58'03" | 15°59'15" | Ionian | Present research | |
| 2003 | 1* | Bova Marina | 37°55'56" | 15°55'06" | Ionian | Present research | |
| 2003 | 1* | Cirò Marina, | 39°21'26" | 17°07'50" | Ionian | Present research (<i>ex alii.</i>) | |
| 2003 | 1* | Torre Nova | | | | | |
| 2003 | 1* | Siderno Marina | 38°16'06" | 16°17'58" | Ionian | Present research (<i>ex alii.</i>) | |
| 2004 | 1* | Bova Marina | 37°55'56" | 15°55'06" | Ionian | Present research | |
| 2004 | 1* | Palizzi Marina | 37°58'03" | 15°59'15" | Ionian | Present research | |
| 2004 | 4* | Brancalone | 37°55'53" | 16°41'20" | Ionian | Present research | |
| Mid-1960s | + | | | | | | |
| 2002 | 1 | <i>Palinuro</i> , Cala del Cefalo | 40°01'31" | 15°19'23" | Tyrrhenian | Bruno (1986) | |
| | | Cellole, Baia Domizia | 41°10'24" | 13°49'50" | Tyrrhenian | Centro Studi Cetacei (2002) | |
| | | | | | | | |
| Campania (n = 1+) Islands (n = 92–93) | 1982 | 1 | Orosei, Berchida | 40°29'58" | 9°49'18" | Tyrrhenian | Whitmore et al. (1991) |
| Sardinia (n = 4) | 1986 | 1 | San Vero Milis, Is Arenas | 40°03'21" | 8°27'31" | Tyrrhenian | and Jesu (1995) |
| | 1994 | 1 | Maracalagonis, | 39°09'15" | 9°23'21" | Tyrrhenian | S. Scarteddu in Cambié (2003) |
| | 2001 | 1 | Torre delle Stelle | | | | M. Piras and S. Nissardi |
| | | Arbus, Piscinas | 39°30'23" | 8°25'08" | Tyrrhenian | (personal communication) | |
| | | | | | | D. Morelli in Fozzi et al. (2002) | |
| | | | | | | | and D. Morelli |
| | | | | | | | (personal communication) |
| Sicily (n = 25) | 1963–1969 | 2 | <i>Marina di Palma</i> , | 37°08'50" | 13°47'38" | Sicilian Channel | Bruno (1970, 1986) |
| | | | Castarozzo di Palma | | | | |
| | 1963–1969 | 1 | <i>Marina di Palma</i> , Focë Palma | 37°09' 59" | 13°43'48" | Sicilian Channel | Bruno (1970) |
| | 1963–1969 | 1 | Vittoria, Scoglitti, Focë Ippari | 36°52'32" | 14°26'19" | Sicilian Channel | Bruno (1986) |
| ? | (1978–1983) | 1* | “Marsala to Mazara”, loc. inc. | 37°43'40" | 12°28'14" | Sicilian Channel | Cocco et al. (1988) |
| ? | (1978–1983) | 1* | Gela, loc. inc. | 37°03'55" | 14°14'40" | Sicilian Channel | Argano and Baldari (1983) |
| ? | (1978–1983) | 1* | <i>Pachino</i> , Capo Passero | 36°41'06" | 15°08'23" | Ionian | Argano and Baldari (1983) |
| | | | | | | | and Cocco et al. (1988) |

Table 3 continued

| Year | Nests n | Locality | Lat N | Long E | Sea | References |
|------|---------|---------------------------------------------------------------------------------------------------------------------------------------|-------------------------------------|-------------------------------------|----------------------------|-------------------------------------------------------------------------------------------------------|
| 1985 | 1 | Augustia, Lido Agnone Marsala, Marausa <i>Noto</i> , Vendicari | 38°18'43" | 15°06'12" | Ionian | L. Lino and G. Insacco (personal communication) Di Palma et al. (1989) |
| 1986 | 1* | | 37°56'24" 36°47'28" | 12°29'08" 15°05'58" | Sicilian Channel Ionian | C. Iapichino in Di Palma et al. (1989) |
| 1986 | 1* | Gela, Femmina Morta, il Biviere | 37°00'98" | 14°19'18" | Sicilian Channel | Di Palma et al. (1989) and G. Turrisi (personal communication) |
| 1990 | 1 | Mazara del Vallo, <i>Bianca Tonnarella</i> Sciaccia, <i>loc. inc.</i> Marina di Palma, Malerba Menfi, <i>loc. inc.</i> | 37°39'33" 37°30'18" 37°08'49" | 12°34'10" 13°04'52" 13°46'47" | Sicilian Channel | Ragonese and Jareb (1992) and Basso (1992) Basso (1992) F. Galia (personal communication) |
| 1990 | 1 | | 37°34'19" | 12°56'35" | Sicilian Channel | A. Napoli in Turrisi and Vaccaio (1997) |
| 1992 | 1 | | 37°30'18" | 13°04'52" | Sicilian Channel | A. Napoli in Turrisi and Vaccaio (1997) |
| 1993 | 1 | Sciaccia, <i>loc. inc.</i> | 37°21'47" | 13°19'27" | Sicilian Channel | F. Galia and G. Salvo (personal communication) and Bombace et al. (2001) |
| 1995 | 1 | Siculiana Marina, Torre Salsa | 36°53'37" | 14°25'38" | Sicilian Channel | G. Insacco (personal communication) |
| 1996 | 1 | Vittoria, Scoglitti, Costa Esperia Realmonte, | 37°17'20" | 13°28'60" | Sicilian Channel | G. Insacco (personal communication) |
| 1996 | 1 | Punta Grande Mazara del Vallo, Capo Feto, il Biscione | 37°39'53" | 12°33'08" | Sicilian Channel | Castelli (1996) |
| 1999 | 1 | Siculiana Marina, Torre Salsa, Foce Salso Realmonte, Punta Grande | 37°21'37" | 13°20'42" | Sicilian Channel | F. Galia (personal communication) |
| 1999 | 1 | | 37°17'20" | 13°28'60" | Sicilian Channel | Insacco et al. (2000) and G. Insacco (personal communication) |

Table 3 continued

| | Year | Nests <i>n</i> | Locality | Lat N | Long E | Sea | References |
|-----------------------------------------|-----------|----------------|----------------------------------|-----------|-----------|------------------|------------------------------------------------------------------------------|
| Eolie, Panarea (<i>n</i> = 1) | 2000 | 1 | Gela, Lido Conchiglia | 37°03'53" | 14°14'41" | Sicilian Channel | G. Insacco (personal communication) |
| Pelagian, Lampedusa (<i>n</i> = 41) | 2002 | 1 | Porto Empedocle, Villa Romana | 37°17'22" | 13°20'19" | Sicilian Channel | Centro Studi Cetacei (2002) and G. Insacco (personal communication) |
| | 2003 | 1 | Sciaccia, <i>loc. inc.</i> | 37°30'18" | 13°04'52" | Sicilian Channel | M. Lo Valvo and F. Galia (personal communication) |
| | 1963–1969 | 1 | Di Tella | 38°38'24" | 15°04'37" | Tyrrhenian | Bruno (1970) |
| | 1975 | 2 | Conigli | 35°30'47" | 12°33'26" | Sicilian Channel | Di Palma (1978), Basso (1992) and G. Boano (personal communication) |
| | 1977 | 2 | Conigli | 35°30'47" | 12°33'26" | Sicilian Channel | Gramenz (1986) |
| | 1978 | 1 | Conigli | 35°30'47" | 12°33'26" | Sicilian Channel | Gramenz (1986) |
| | 1983 | 1 | Conigli | 35°30'47" | 12°33'26" | Sicilian Channel | Gramenz (1986) |
| | 1985 | 1 | Conigli | 35°30'47" | 12°33'26" | Sicilian Channel | Gramenz (1986) and Bassi (1992) |
| | 1986 | 1* | Conigli | 35°30'47" | 12°33'26" | Sicilian Channel | Di Palma et al. (1989) |
| | 1990 | 1 | Conigli | 35°30'47" | 12°33'26" | Sicilian Channel | Basso (1992) |
| | 1991 | 5 | Conigli | 35°30'47" | 12°33'26" | Sicilian Channel | D. Freggi (personal communication) |
| | 1994 | 5* | Conigli | 35°30'47" | 12°33'26" | Sicilian Channel | Freggi (1997) |
| | 1995 | 1* | Conigli | 35°30'47" | 12°33'26" | Sicilian Channel | Freggi (1997) |
| | 1996 | 4* | Conigli | 35°30'47" | 12°33'26" | Sicilian Channel | Freggi (1997) |
| | 1998 | 3* | Conigli | 35°30'47" | 12°33'26" | Sicilian Channel | Bombace et al. (2001) |
| | 1999 | 2* | Conigli | 35°30'47" | 12°33'26" | Sicilian Channel | Bombace et al. (2001) |
| | 2000 | 2* | Conigli | 35°30'47" | 12°33'26" | Sicilian Channel | Bombace et al. (2001) |
| | 2002 | 7* | Conigli | 35°30'47" | 12°33'26" | Sicilian Channel | Piovano et al. (in press) |
| | 2004 | 3* | Conigli | 35°30'47" | 12°33'26" | Sicilian Channel | Piovano et al. (in press) |
| Pelagian, Linosa (<i>n</i> = 21–22) | 1986 | 2* | Pozzolana di Ponente | 35°51'48" | 12°51'17" | Sicilian Channel | Di Palma et al. (1989) |

Table 3 continued

| Year | Nests <i>n</i> | Locality | Lat N | Long E | Sea | References |
|------|----------------|----------------------|-----------|-----------|------------------|---------------------------------------|
| 1992 | 1–2 | Pozzolana di Ponente | 35°51'48" | 12°51'17" | Sicilian Channel | D. Freggi (personal communication) |
| 1994 | 6* | Pozzolana di Ponente | 35°51'48" | 12°51'17" | Sicilian Channel | Dominici et al. (2000) |
| 1996 | 3* | Pozzolana di Ponente | 35°51'48" | 12°51'17" | Sicilian Channel | Dominici et al. (2000) |
| 1998 | 2* | Pozzolana di Ponente | 35°51'48" | 12°51'17" | Sicilian Channel | Dominici et al. (2000) |
| 2001 | 3* | Pozzolana di Ponente | 35°51'48" | 12°51'17" | Sicilian Channel | Piovano et al. (in press) |
| 2002 | 1* | Pozzolana di Ponente | 35°51'48" | 12°51'17" | Sicilian Channel | Piovano et al. (in press) |
| 2004 | 3* | Pozzolana di Ponente | 35°51'48" | 12°51'17" | Sicilian Channel | Piovano et al. (in press) |

Asterisks (column: Nests *n*) refer to the nests found during monitoring projects. In *italic* (column: Locality) are shown place-names not quoted in original references, but included as complementary geographical information (municipality and/or place name next to the beach). Whenever place name could not be specified, notation *locus incognitus* (*loc. inc.*) was given

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Benefits of habitat restoration to small mammal diversity and abundance in a pastoral agricultural landscape in mid-Wales

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Abstract Changes in agricultural practice are predicted across the UK following agricultural reform driven by government policy. The suitability of agri-environment schemes for many species is currently debated because limited quantitative data are collected. In order to understand the changes to biodiversity due to agri-environment schemes, there is a need for studies to not just compare biodiversity and species composition in and out of agri-environment areas, but to factor in the influence of temporal habitat changes. In this study, we investigate the suitability of an agri-environment initiative to support and enhance a small mammal fauna among pastoral hill farms in mid-Wales. Grazed and ungrazed woodlands, riparian habitats, and broadleaf plantations, were compared for small mammal abundance and diversity following a trapping study. Mammal diversity was similar across habitats, though abundance varied significantly. A principle component analysis identified that mammal abundance clustered into three main habitat groups separated by seral stage (early, mid, late). No relationship between mammal abundance and stock grazing was found. A canonical correspondence analysis confirmed that vegetation structure was important in explaining the distribution of captures of mammal species across the landscape. The results for habitat type, and habitat context, suggest that a mix of vegetation seral stages, reflecting a varied vegetation structure, is important to maintain small mammal diversity and abundance across the study area. Heterogeneity in structural diversity at the landscape scale is important to maintain a variety of ground-dwelling mammal species, and particularly because trends in countryside surveys show that woodlands are skewed towards late seral stages.

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Habitat heterogeneity can be maintained because the hill farms neighbour each other, and the farmers co-operate as a group to manage the landscape. Habitat diversity is therefore possible. These results help us to advocate, and anticipate, the benefits of groups of farms within a landscape.

Keywords Agri-environment scheme · Bank vole · Common shrew · Grazing · Landscape ecology · Restoration ecology · Small mammals · Woodland · Wood mouse · Yellow-neck mouse

Introduction

The intensification of agriculture has had an important impact on the European landscape that has been constructed by man and his management practices since the last ice-age. The realisation of this impact on biodiversity and on a range of species has led to several responses from the British and European governments. The European Union (EU) agricultural policy first addressed these agricultural issues in 1985 by introducing a set of measures to efficiently protect the environment (Kleijn and Sutherland 2003). In the UK, the recent 2003 reform of the common agricultural policy (CAP) for example, has implemented a new set of policies aimed to improve environmental protection of agricultural land. The reform introduces the decoupling legislation where farmers will be paid a single area payment to eliminate overstocking and intensive productions as well as cross-compliance which will oblige farmers to meet certain environmental standards before subsidy payments are made. In addition, the modulation of the CAP will allow more funds to go towards initiatives that enhance environmental protection in agricultural landscapes (DEFRA 2003). Presently, the main approach to address the agri-environmental issues remains the implementation of agri-environment schemes (Sutherland 2002).

Agri-environment schemes are the response by the British government to reduce the negative impacts of agriculture in Britain. Reliable evaluations of the benefits of these schemes for wildlife are few (Kleijn and Sutherland 2003). Furthermore, the efficacy of agri-environment schemes for supporting or enhancing biological, social or historic features has been questioned (Kleijn et al. 2001; Carey et al. 2005). In order to understand the changes occurring on agricultural land due to agri-environment schemes, there is a need for studies to not just compare biodiversity and species composition in and out of agri-environment areas, but to factor in the influence of temporal habitat changes (Kleijn and Sutherland 2003).

Recent studies on invertebrate and bird communities within and outside agri-environment schemes have stressed the importance of maintaining or restoring natural habitat for conserving these taxa (e.g. Hawthorne et al. 1998; Wakeham-Dawson et al. 1998; Pywell et al. 2004; Aviron et al. 2005); however, much less is known about the effectiveness of these schemes for small mammal assemblages (Kleijn and Sutherland 2003; Smith et al. 2005). Small mammals are useful indicators of environmental health, biodiversity or agricultural change (Flowerdew et al. 2004), and play an essential role for mammalian and avian predators (Love et al. 2000; Moore et al. 2003). Long term trapping studies across parts of the UK have suggested declining trends of some small mammal species over time (Harris et al. 1995). This is thought to be because farming management mainly results in a reduction or

loss of vegetation structure and in the fragmentation of available habitat (Jacob 2003).

In Wales, agri-environment policy changes have shifted. Initially, farmers were encouraged to list their lands as Environmentally Sensitive Areas (ESAs) which aimed to maintain nationally important landscapes, wildlife or cultural features on their farms. Recently, schemes such as Tir Gofal have superseded ESAs where the ethos now focuses not just on habitat maintenance, but on habitat restoration and recreation on farmland, in addition to creating opportunities for farmers to integrate their management with forestry and woodland grants. As with other agri-environment initiatives, whilst these strategies to maintain and restore habitat to improve biodiversity are laudable, there are concerns relating to the value of these schemes to the agricultural landscape because of a lack of quantitative data (Herzog 2005). A community agri-environment initiative such as one utilized in this study at Pontbren in mid-Wales could allow us to anticipate what the long-term effects of agri-environment schemes may be for a variety of biota.

Our main hypothesis was that small mammal diversity and abundance would be related to the age of a habitat. If this were true, we would expect that species richness and abundance should be higher as the age of the restored habitat increased. We further hypothesized that habitats grazed by stock would support a less diverse, and less abundant, small mammal fauna based upon the findings of grazing studies elsewhere (Smit et al. 2001). We compare small mammal abundance between fragments of different age reflecting different habitat restoration procedures. We consider the implications of these findings within the context of farmland habitat restoration policy for small ground-dwelling mammals.

Methods

Study sites and landscape context

The Pontbren landscape in mid-Wales comprises a farming area which fits within an agri-environment framework, and provides a good example of a modern conservation approach in agriculture. Farming occurs among pastoral hill farms, and sheep (and to a lesser extent, cattle) provide the main source of income on what is primarily a pasture landscape. Ten farming families living on adjacent farms, and encompassing a total area of 1,000 ha, established the ‘Pontbren Group’. The aim of this scheme is to provide a sustainable approach to farming, diversify their farming practices, and increase their economic returns. The farmers have *voluntarily* changed farming practices by limiting grazing through fencing, reducing overall sheep and cattle densities by 25% (from 1.9 stock units ha^{-1} in the mid-1990s to as low as 1.2 stock units ha^{-1} in 2004), and restoring woodlands, wetlands and riverbanks by planting trees. For example, wooded areas have increased from 1% in 1993 to approximately 5% in 2004, and with a forecasted increase to 15% by 2008. These landscape changes have been shown to have significant potential for hydrological and soil protection (Carroll et al. 2004). Historical information available on the age when broadleaf plantings commenced, or when stock exclusion fencing was erected around habitat fragments, provides us with an appropriate landscape to compare changes of taxonomic groups in and out of managed habitats

(and importantly, among neighbouring, conventional farming practices) yet within the spatial confines of one landscape. Within the context of agri-environment schemes across Europe, it is therefore timely to ask and predict what changes may be envisaged to mammal species following this specific component of the Pontbren approach.

Habitats were selected for trapping based upon a variety of modified and unmodified fragments found within the Pontbren landscape. Fragments represented both linear (riparian) and nonlinear (farm and wood plots) shapes, but for this project shape was not considered in the research design because it has been found to make little difference to small mammal abundance and diversity among farmed lands (Tattersall et al. 2002). Habitat fragments occur scattered among a matrix of open, roughly-grazed fields. Fragment sizes ranged from 0.2–30 ha. Fragments were predominately broad-leaved. Where possible, sites were selected to occur on separate farms, and replicates for each habitat category were sampled for small mammals in different weeks to minimize differences between captures in habitats associated with weather and season.

In total 26 sites, comprising nine habitats, were selected to sample for small mammals based on stock (sheep) grazing presence or absence, or whether habitats represented riparian, broadleaf plantation, open pasture, or woodland vegetation fragments. With the exception of a regenerating broadleaf woodland of at least 50 years of age (of which there was only one site available), other habitats were replicated at least twice depending upon available and suitable replicates in the landscape. Brief habitat descriptions follow and are presented in Table 1:

Habitat a: Grazed woodlands of broadleaf with dense canopy cover largely made up of oak species, moderate sub canopy and understorey cover, and a relatively short grass cover. These sites have been proposed for future fencing to exclude sheep.

Habitat b: High-intensity grazed unplanted fields made up of very short grass species palatable to livestock.

Habitat c: Fragments comprising broadleaf woodland that have been left to regenerate for 1–3 years. Moderate canopy cover. A thick and tall grass cover occurs but there are neither obvious sub-canopy nor understorey layers.

Habitat d: Unfenced riparian sites comprising a dense subcanopy and understorey cover, and sparse to moderate canopy.

Table 1 Habitat descriptions of sites that were selected for mammal trapping across the Pontbren landscape in 2004

| Category | Habitat code | Habitat age & condition | No. replicates | Area ¹ (ha) | Stock grazing |
|----------------------|--------------|----------------------------|----------------|------------------------|---------------|
| Riparian | e | Mean 2 year regenerating | 2 | 0.34 (0.30) | No |
| | i | Mean 6.5 year regenerating | 3 | 0.83 (0.38) | No |
| | d | > 10 year | 2 | 0.23 (0.05) | Yes |
| Woodland | c | Mean 2 year regenerating | 4 | 0.31 (0.42) | No |
| | a | > 10 year | 3 | 1.07 (0.90) | Yes |
| | f | 50 year regenerating | 1 | 30 | No |
| Pasture | b | Pasture | 3 | 2.21 (1.26) | Yes |
| Plantation | g | 2 year | 4 | 1.26 (2.05) | No |
| | h | Mean 8.5 year | 4 | 0.28 (0.11) | No |
| Total trapping sites | | | 26 | | |

¹ representing mean (\pm SD)

Habitat e: Fenced riparian sites regenerating since 2002 and comprising broadleaf tree species. Some sites are covered by a canopy and other sites are open with little subcanopy and understorey cover, and with tall grass species.

Habitat f: Fenced, regenerating broad-leaved woodland with a dense understorey layer and tall bramble and ferns. Dense litter layer.

Habitat g: Recently fenced broadleaf plantations containing young trees and tall grass species with sparse understorey of scattered young trees around 1 m height.

Habitat h: Fenced broadleaf plantations of 8–9 years forming a dense subcanopy layer. Ferns and bramble comprise a thick understorey.

Habitat i: Fenced riparian sites of regenerating broadleaf trees 5–10 years in age with moderate to dense subcanopy and understorey layers.

Habitat context was considered in addition to individual habitat to assess whether the proximity of one habitat to nearby habitats affected mammal abundance. This approach considers the grain at which small mammals may respond to landscape pattern. Spatial scale was based upon average home ranges used in woodlands by small mammals found across the UK viz. 0.1–0.2 ha for bank voles (Alibhai and Gipps 1991), 1.4 ha for field voles (Gipps and Alibhai 1991), 0.5 ha for wood mice (Tattersall and MacDonald 2002) and 0.1 ha for common shrew (Churchfield 1991). A map of the Pontbren area was digitised into a geographic information system. Borders of three widths representing 50, 100, and 150 m were created around each habitat to accommodate the various distances potentially moved by small mammals. The relative occurrence of five descriptors of habitat context was then calculated (see below).

Survey protocol

Trapping occurred between June and August 2004. Longworth live-capture traps were used to capture small mammals. Each habitat contained 20 traps, though for one large (ca. 30 ha) site, 60 traps were set each night in a grid. A variable trapping regime was applied. At small sites (< 1.5 ha, $n = 20$), the traps saturated the habitat area and were spaced at 5 m intervals. At larger sites ($n = 6$), the traps were positioned in a grid with four rows spaced at 20 m intervals, and each row with five traps spaced at 20 m intervals. For (linear) riparian sites, a transect line set 1 m in from the river was used to position traps every 10 m. Bait comprised a mixture of peanut butter and oats, and hay was placed in the traps for bedding. At each site, traps were opened daily from 1600 h for four consecutive nights. Traps were checked each morning from 0600 h, and were kept closed during the day. Animals caught were identified to species, sexed, weighed to the nearest gram (using PesolaTM scales), marked by fur clipping to identify later recapture, and released at the site of capture.

A vegetation structural assessment was carried out at each site using quadrats. Quadrat size depended upon habitat type: 10 × 10 m quadrats were used in woodland habitats and those sites with dense vegetation, while 2 × 2 m quadrats were used in all other habitat types such as fields and riparian sites where structural vegetation height was relatively low. In order to get a representative estimate of vegetation cover for each site, one quadrat was taken for each row of the gridlines and one per five traps for the transect lines. In each quadrat, the percentage cover of dominant vegetation species was visually estimated for the canopy (> 10 m height),

sub-canopy (2–9 m), understorey (0.5–2 m) and ground (< 0.5 m, including leaf litter) layers during mid-summer.

Data analyses

Mammal abundance was compared between habitats by standardizing the number of small mammals known-to-be-alive (KTBA) (Krebs 1966) to captures per 100 trap-nights (where one trap opened over one night equals one trap-night). Calculations excluded those traps that had shut over-night without capturing anything. All statistical analyses were conducted using the computer package GenStat® v6.1 (Payne 2002). Significant difference was assumed at the 5% level of significance.

A Principal Component Analysis (PCA) was used to look for patterns of small mammal distribution across the 26 sites sampled in the Pontbren landscape. A correlation matrix (Manly 1994) was used because captures between habitats had different variances. A plot of principal components 1 and 2 enabled habitats to be clustered into groups. A one-way analysis of variance (ANOVA) was then used to test the significance of these groups, with Species as the response variable and Group as the treatment. Pairwise comparisons of means were analysed using Fisher's Least Significant Difference (LSD).

Canonical Correspondence Analysis (CCA, ter Braak 1995) is a widely applied method for directly relating patterns in species richness or abundance to underlying environmental gradients. CCA and partial CCA analysis were conducted with the program CANOCO vs4.5 (ter Braak and Smilauer 2002). In the analysis presented here it identifies how the abundance of mammal species responds to parameters of vegetation density (cover), to grazing, and to landscape context. CCA was used to relate the abundance of each species to four habitat structural variables (percentage cover of dominant vegetation for the canopy, sub-canopy, understorey and ground layers), and to the occurrence of stock grazing. Additionally, landscape context (proportion of early-seral habitats, proportion of mid-seral habitats, proportion of late-seral habitats, proportion of all three habitats regardless of age group excluding pasture, and proportion of pasture habitats only) was considered at three spatial scales as explained earlier.

As part of the analysis, step-wise forward selection was used on each explanatory variable separately to eliminate those habitat and landscape variables which did not explain significant ($p < 0.05$) variation (tested with 200 Monte Carlo permutations) (Hope 1968). The interset correlations of the environmental variables with the significant axes were examined under a global CCA to determine those environmental variables selected previously that were significantly correlated with the axes (ter Braak 1995). If collinearity was observed between variables (in this case, where correlations ≥ 0.7), those with the higher correlation were included in a partial CCA. The results are displayed as a visual ordination diagram showing (a) how species are positioned in relation to the main axes according to their abundances and (b) the strength of the habitat variables and landscape descriptors in explaining the axes. Hence, these ordination diagrams convey information at both the habitat level and the individual species level, and within the context of the landscape.

Results

Small mammal community structure

Trapping success for small mammals was 14% representing 232 individual captures from 1676 trap-nights (Table 2). Average mammal captures were highest among regenerating riparian habitats aged 5–10 years, and broadleaf plantations aged 8–9 years. Low captures occurred in fenced riparian habitats (regenerating for 1–3 years) and fenced (1–3 year old) broadleaf plantations. Importantly, no small mammals were captured in grazed pastures.

Six species of small mammal were trapped at Pontbren: yellow-necked mouse *Apodemus flavicollis*, bank vole *Clethrionomys glareolus*, field vole *Microtus agrestis*, common shrew *Sorex araneus*, wood mouse *Apodemus sylvaticus*, and water shrew *Neomys fodiens*. A plot of total abundance of each species against the number of sites shows that wood mice were widespread and abundant, whereas field voles, common shrews, bank voles and to a lesser extent, yellow-necked mice were common but not widely distributed (Fig. 1). Only one individual capture of a water shrew occurred (in grazed riparian habitat > 10 years in age), suggesting a locally rare species, and it is not considered further in analyses.

Relative spatial distribution of captures among habitats

The distribution of captures for the five common species was compared between nine habitats across the Pontbren landscape using a principal component analysis (PCA). The first two axes explained over 75% of the total variance. Bank voles, field voles, wood mice, and common shrews have a similar habitat contribution along principal component axis 1 and this may represent similar habitat requirements

Table 2 Small mammal abundance (excluding recaptures), mean small mammal abundance per 100 trap-nights and associated standard error (SE), and number of active traps in nine different trapping habitats across Pontbren

| Habitat | Number of active traps | Total mammal abundance | Mean abundance | SE |
|------------------------------------------------|------------------------|------------------------|----------------|-----|
| > 10 year riparian (grazed) | 161 | 25 | 15.5 | 2.9 |
| Mean 2 year regenerating riparian (ungrazed) | 169 | 13 | 7.7 | 2.1 |
| Mean 6.5 year regenerating riparian (ungrazed) | 150 | 32 | 21.3 | 2.4 |
| > 10 year woodlands (grazed) | 163 | 22 | 13.5 | 2.7 |
| Mean 2 year regenerating woodland (ungrazed) | 224 | 23 | 10.8 | 2.1 |
| 50 year regenerating woodland (ungrazed) | 177 | 27 | 15.3 | 2.7 |
| Pasture (grazed) | 180 | 0 | 0 | 0 |
| 2 year broadleaf plantation (ungrazed) | 228 | 29 | 12.7 | 2.2 |
| Mean 8.5 year broadleaf plantation (ungrazed) | 224 | 61 | 27.2 | 3.0 |
| Total | 1676 | 232 | | |

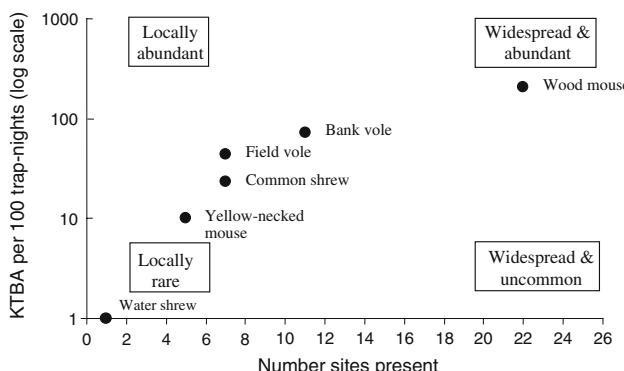


Fig. 1 Relationship between abundance of individuals (known to be alive, KTBA) and frequency of occurrence of six species of small mammals captured in 26 habitats across Pontbren

Table 3 Summary of principal component analysis conducted using a correlation matrix. Components 1 and 2 explained over 75% of the total variance

| | PC1 | PC2 |
|------------------------|--------|--------|
| Latent roots | 2.37 | 1.45 |
| Percent variance | 47.56 | 29.09 |
| Cumulative % variation | 47.56 | 76.65 |
| Latent vectors | | |
| Wood mouse | 0.576 | 0.157 |
| Bank vole | 0.510 | -0.279 |
| Yellow-necked mouse | 0.231 | 0.705 |
| Field vole | -0.423 | -0.292 |
| Common shrew | 0.418 | -0.561 |

(Table 3). Yellow-necked mice were important in explaining variation along principal component axis 2 (Table 3).

A scaling scatterplot of component scores for each habitat from the PCA shows three main habitat groups along principal components 1 and 2 consistent with three habitat seral (regeneration) stages (Fig. 2): early (habitats b, c, e, g together representing grazed fields, and ungrazed pioneer regenerating habitats 1–3 years old), mid (habitats h and i representing 5–10 year regenerating sites), and late (habitats a, d, f representing regenerating or mature sites at least 10 years in age). The biplot, including latent vectors for the five mammal species, shows that yellow-necked mice increase gradually in abundance in the direction of late seral habitats, field voles among early seral habitats, and bank voles, wood mice and common shrews among mid-seral habitats. There is no clear grouping of small mammals between grazed and ungrazed habitats.

Pairwise comparisons of the means using the Fisher's LSD revealed that most mammal captures occurred in mid-seral habitats, followed by late and early seral habitats (Table 4). Specifically, captures of yellow-necked mice were significantly higher on average among late seral habitat than in either mid or early seral habitats (Table 4). In contrast, wood mice, bank voles and common shrews were captured more often among mid-seral habitats than either late or early seral habitats (Table 4). Large variation in captures of field voles across habitats reflects the LSD

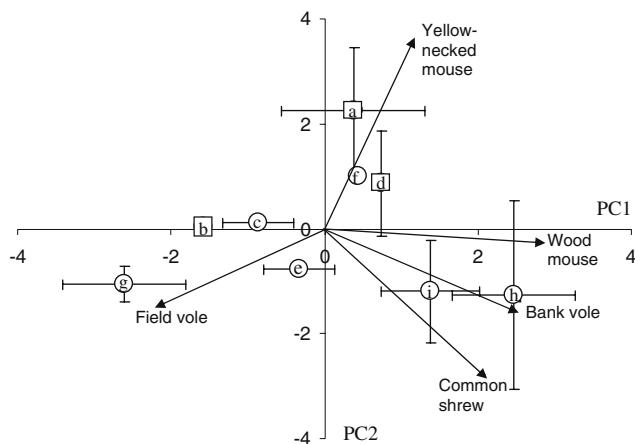


Fig. 2 Principal component analysis biplot of nine habitats using a correlation matrix of association between small mammal species abundance. Values represent means and standard deviations. Vectors of loadings for each mammal species have been included, scaled by five (represented as arrows). Areas where grazing has been excluded are represented as circles, and grazed areas are represented as squares. Habitats are coded based on the categories in Table 1

Table 4 Mean (\pm SD) abundance, and results of one-way ANOVA and Fisher's Least Significant Difference, for five mammal species across each habitat age group (identified by Principal Component Analysis) at Pontbren. Mammal abundance has been standardized to captures per 100 trapnights

| Habitat age group | Wood Mouse | Bank vole | Yellow-necked Mouse | Field vole | Common Shrew | All species |
|-------------------|---------------------------|--------------------------|--------------------------|--------------------------|--------------------------|---------------------------|
| Early $n = 13$ | 3.37 ^b (4.44) | 0.13 ^b (0.47) | 0 ^b | 3.23 ^a (5.79) | 0.41 ^b (0.78) | 7.15 ^b (4.98) |
| Mid $n = 7$ | 15.03 ^a (2.17) | 8.58 ^a (4.07) | 0.26 ^b (0.67) | 0.26 ^a (0.68) | 2.35 ^a (2.04) | 24.49 ^a (6.20) |
| Late $n = 6$ | 9.60 ^b (2.47) | 1.67 ^b (2.41) | 1.40 ^a (1.31) | 0 ^b | 0.29 ^b (0.71) | 12.31 ^c (2.51) |
| <i>F</i> | 20.20 | 45.96 | 14.66 | 2.38 | 4.44 | 15.43 |
| <i>P</i> | < 0.001 | < 0.001 | < 0.001 | 0.115 | 0.023 | 0.010 |

Means that were significantly different based on LSD are labeled with different letters

result which indicates that mean captures of this species were not significantly different among the three habitat groups identified by PCA.

Effects of habitat structure and landscape context on mammal captures

Global CCA revealed that grazing as an explanatory variable was not sufficiently significant to describe patterns of mammal distributions, and was excluded from further analysis. Explanatory variables considered in the partial CCA included: vegetation structure (ground layer, understorey, subcanopy, canopy), and landscape context (proportion of mid and late seral habitats within 100 m of mid or late seral habitats, respectively).

A summary of the CCA output (Table 5) following global CCA shows that the first two axes explained over 80% of the species-habitat variation (Monte Carlo permutations, first axis: $p = 0.018$; all axes: $p = 0.032$). The species-habitat

Table 5 Results of a partial canonical correspondence analysis for small mammal abundance data for the habitats sampled across Pontbren

| Statistic | Axis 1 | Axis 2 | Axis 3 | Axis 4 | Total variance |
|---------------------------------------------------|--------|--------|--------|--------|----------------|
| Eigenvalue | 0.473 | 0.095 | 0.042 | 0.001 | 0.747 |
| Species-habitat correlation | 0.988 | 0.891 | 0.617 | 0.138 | |
| Cumulative percentage variance of species data | 63.3 | 76.0 | 81.6 | 81.7 | |
| of species-habitat relation | 77.5 | 93.0 | 99.9 | 100 | |
| Sum of all eigenvalues | | | | | 0.747 |
| Sum of all canonical eigenvalues | | | | | 0.611 |

correlations, indicating the ability of habitat variables to explain the variation in mammal abundance, were 0.988 for the first axis and 0.891 for the second; these high correlations suggest that most of the variation in mammal abundance can be explained by these structural habitat variables. The proportion of mid and late seral habitat contexts within 100 m of other mid or late seral habitats, respectively, had the strongest influence on mammal abundances (8.5% and 5.7% of variance, respectively) compared to the other habitat context units assessed.

The first CCA axis was positively correlated with, and thus influenced by, ground cover and it was most negatively correlated with canopy cover. It also differentiated the proportion of mid seral habitat contexts (100 m) from late seral habitat contexts (100 m) (Fig. 3). The habitat variables correlated with this first axis describe a vegetation structural gradient from ground-level at the positive end to above-ground at the negative end. Field voles had high positive scores on the first axis reflecting an association of captures in sites with ground cover. Captures of the remaining four mammal species were associated with above-ground canopy cover and with mid and late seral habitat contexts (100 m).

Habitat variables correlated with the second axis reflect above-ground vegetation structure, being most strongly correlated with subcanopy cover and mid seral habitat contexts (100 m) in one direction and canopy cover and late seral habitat contexts (100 m) in the opposite direction (Fig. 3). The ordination shows that yellow-necked mice and wood mice cluster with habitats containing a canopy cover and little ground cover, and where habitat context consists of late seral habitats within 100 m of each other. Common shrews and bank voles were associated with habitats containing understorey and subcanopy cover, and where habitat context consists of mid-seral habitats within 100 m of each other.

Discussion

We sought to compare the diversity and abundance of small terrestrial mammals between restored and unrestored fragmented habitats within the context of the effectiveness of agri-environment schemes to maintain biodiversity on pastoral farmland. Our first hypothesis that mammal species richness and abundance would increase with the age of the vegetation was not supported. Instead, species richness and abundance varied with vegetation seral stage, and this corresponded to vegetation structural diversity. More small mammals were captured in mid-seral habitats, although early and late seral habitats also supported a complement of small

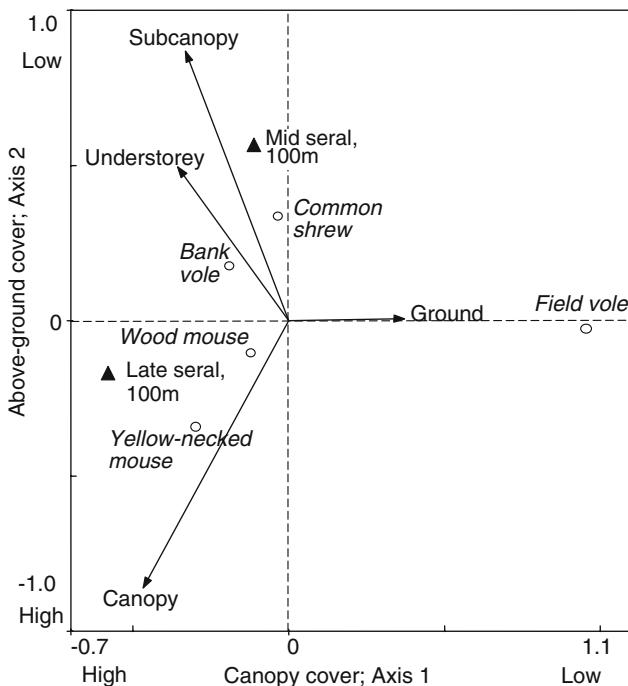


Fig. 3 Biplot of the first and second axes of a canonical correspondence analysis ordination of habitat variables in relation to species distribution, habitat type, and habitat context (proportion of late or mid seral habitats within 100 m of equivalent age habitats). Arrows represent habitat variables included in the model which best represent the distribution of captures of mammal species at Pontbren. Arrow length represents the relative importance of each habitat variable in the model, and the direction of each arrow relative to the axes indicates its correlation strength to each axis. The location of each mammal species (open circles) represents the habitat or habitat context (solid triangles) associated with its occurrence

mammals. Specifically, field voles showed no particular association with a seral stage or habitat context but were highly correlated with habitats exhibiting a prominent ground layer. Bank voles, wood mice and common shrews were primarily (though not exclusively) associated with mid-seral habitats with a dense subcanopy and understorey cover. Furthermore, bank voles and common shrews were associated with a habitat context where mid-seral habitats were within 100 m of each other. In contrast, wood mice and yellow-necked mice were associated most with a habitat context where late-seral habitats were within 100 m of each other. This is in accord with known bank vole and wood mouse habits (Geuse 1985; Churchfield et al. 1997), though common shrews are also reported to occupy grassland habitats in the UK (Churchfield et al. 1997). Wood mice were the most abundant species trapped during our study, and are a common species across farmland habitats (Burke and Taylor 2002). Finally, yellow-necked mice were only captured in late-seral habitats with a canopy cover, consistent with similar patterns of distribution elsewhere (Marsh and Harris 2000; Marsh et al. 2001). Vegetation cover affords small mammals protection from predators, and provides a suitable microclimate and food resources. An abundant small mammal fauna (in particular, *Microtus* sp.) provides important food

resources for mammalian and avian predators, some of which are becoming locally rare in the UK (eg. barn owls *Tyto alba*).

Our second hypothesis investigated the effects of grazing on small mammals. At Pontbren no small mammals were captured among fields grazed by sheep and where an above-ground vegetation layer was absent, indicating the immediate promotion of a small mammal community when these fields are planted with trees. This is important because open fields seem to represent an impermeable matrix within the Pontbren landscape where there is no field edge for mammals to move in. However, small mammals were captured among woodland habitats where stock had access, suggesting that some species of native mammals will persist in habitat with a favourable number of stock. The negative impact of grazing stock on small mammals is reported elsewhere. For example, Putman et al. (1989) found significant differences in rodent density between grazed and ungrazed woodlands, and Bokdam et al. (2001) report that exclusion of stock in grazed habitats had a clear positive impact on rodent densities. At Pontbren, lack of any mammal captures in pasture fields suggests that linear connections between habitats (riparian or hedgerow) will form important networks which connect habitats for small mammals that move considerable distances (Fitzgibbon 1997). Importantly, there were other habitats in Pontbren where stock had access and where small mammals were captured. The reason is likely to be associated with stock which occupied these fragments for shelter rather than for grazing, and complemented by low stocking densities, this did not appear to overtly affect the captures (and implicitly, abundance) of the small mammal community. Consequently, an above-ground vegetation cover was able to develop which seems to have been important for the persistence of some species. On the other hand, fields are constantly grazed making conditions for small mammals inappropriate.

It is unlikely that all small mammals are totally reliant upon the isolated habitat fragments sampled (Fitzgibbon 1997). What is important in this study is to consider the totality of the agricultural land under an agri-environment scheme rather than focus at the level of the individual habitat or farm plot. The contribution of additional linear habitats such as hedgerows to the small mammal community at Pontbren remains unknown but is recognized to provide important connecting habitat across the wider landscape (Harris and Woollard 1990). Riparian habitats were clearly used by all six mammal species (including water shrew), and hedgerow restoration is also on the Pontbren habitat management agenda.

A diversity of habitats is an important way to create a range of habitat niches containing different prey densities so foragers can concentrate on the best patches initially but can also exploit other patches as resources become depleted (Stephens et al. 2003). We stress that this heterogeneity in structural diversity is at the landscape scale which, at Pontbren, can work because the farms are contiguous and the farmers cooperate as a group to manage the area. Habitat diversity is therefore possible. The Pontbren agri-environment landscape provides habitat heterogeneity by maintaining a range of habitat types to support a range of small mammal species. A mosaic of habitats has also been shown to benefit birds, ground beetles, and butterflies (Galbraith 1988; Sunderland and Samu 2000; Ostman et al. 2001).

For farmed landscapes like in this study, this patchwork of habitat ages is a consequence of a staggered approach to restoring habitat over time rather than a conscious effort to maintain heterogeneity. In retrospect, this temporal separation demonstrates advantages for a small mammal fauna. Indeed, fragments as small as

0.13 ha were able to support small mammals and presumably, provide appropriate refugia for them. Future management at Pontbren aims towards coppicing the woodlands as a source of timber at irregular cycles (5–10 years, 40 years) to maintain low-level shelter (short rotation coppice) and for timber production (long rotation coppice). There are implications to mammal abundance, and potentially diversity, across the landscape. As discussed by Moore et al. (2003) and Benton et al. (2003), the way forward would be to determine how planted woodlands can be best designed and maintained to benefit biodiversity such as small mammals and their prey.

Maintaining habitat heterogeneity is important when placed within the context of recent countryside surveys in the UK (Haines-Young et al. 2000). Trends show that woodlands are becoming less diverse with time. In addition, these surveys have found there is a decline in plant species richness among woodlands in England and Wales, implicit in an increase in vegetation succession favouring late-seral (and shade-tolerant) plant species. This trend has larger implications to small mammal communities and their abundance if structurally diverse woodlands of variable age continue to become skewed towards the late seral stages. Moving away from a landscape with a mosaic of habitats may have serious impacts upon ground-dwelling small mammals.

Wildlife benefits are not the only factor to be considered to assess the performance of the Pontbren agri-environment landscape. Another focuses on the social well-being of the families that live there. Wildlife benefits encourage farmers to be motivated to restoring the land through a sense off stewardship rather than being driven by financial incentives (Schmitzberger et al. 2005). The Pontbren initiative is a rare example of community partnership where the idea of improving agricultural land has come from the farmers themselves and not in response to a government grant. The farming community is working together towards a more sustainable way of farming by using its own initiative and interests in conservation. By committing themselves to the management of the countryside through the plantation of native trees and the restoration of woodlands and riparian habitats, the Pontbren farmers have not only managed to support their own livelihood but also to increase the conservation value of their land as reflected in small terrestrial mammals, and has benefited soil and water resources (Carroll et al. 2004).

Conservation implications

Our results show that the full range of small mammal species is found if a variety of habitats of variable vegetation structure and landscape context are maintained. There is a need for habitat heterogeneity, and this promotes biodiversity (Benton et al. 2003). The evidence of the benefits to small mammals of past habitat restoration on Pontbren have clear, positive implications for woodland restoration initiatives across Wales and elsewhere. Woodlands currently occupy approximately 5% of the total farm area of Pontbren, and the aim is to increase this to 15%. From a farmland management and policy perspective, it may be possible to develop measures which target habitat heterogeneity in terms of structural diversity within a landscape and which can act as a surrogate for small mammal abundance. Comparisons between landscapes may be useful to see the benefits for species richness and indeed, develop hypotheses of habitat diversity thresholds. To conclude, our advice to farmers restoring habitat at pastoral sites where stocking rates are

moderate is to maximise habitat heterogeneity within the landscape that supports a structurally-complex vegetation mosaic and in turn, a diverse, abundant small mammal fauna. Supporting an abundant small mammal fauna will also maintain local populations of rare species such as yellow-necked mice, in addition to predatory birds and mammals on these agricultural lands.

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Modelling habitat use and distribution of golden eagles *Aquila chrysaetos* in a low-density area of the Iberian Peninsula

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Abstract We analyse the current situation of the Golden eagle (*Aquila chrysaetos*) in the region of Galicia in NW Spain. At present, the entire Galician population (five pairs) is located within an area of about 2000 km² in the province of Ourense. To identify high-priority areas for golden eagle conservation, we derived predictive models of habitat suitability using logistic regression and a Geographic Information System (GIS). Specifically, to model the distribution of the breeding population we considered topographic features, land use and degree of humanization, using a 10 × 10 km grid. Presence/absence of golden eagle nests was used as the dependent variable; analyses were performed both considering current nesting areas and considering old nesting areas (1960s and 70s). At the spatial scale considered, the best predictors of habitat suitability for breeding were topographical variables indicative of rugged relief. For current nesting areas the most parsimonious model included maximum altitude. We consider that the predictive models obtained may be of use for the monitoring and conservation management of the golden eagle population in this region. Conservation problems associated with habitat constraints such as food supply, availability of nesting sites, changes in land use and human disturbance are discussed.

Keywords *Aquila chrysaetos* · Conservation · Golden eagle · Habitat use · Modelling · Persecution · Poison

Introduction

Analyses of the relationships between species and their habitats are essential for establishing appropriate conservation management plans (Morrison et al. 1998;

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Jones 2001). In line with this, modelling studies of the distribution of raptors and other vertebrate species have become more common in recent years, given their utility as management tools (see e.g. Sánchez-Zapata and Calvo 1999; Naves et al. 2003; Sergio et al. 2003; Bustamante and Seoane 2004), although certainly this approach has significant limitations (Fielding and Haworth 1995; Beutel et al. 1999; Brito et al. 1999; Seoane and Bustamante 2001; Rushton et al. 2004).

Raptors are typically selective with regard to habitat, especially breeding and hunting areas (Janes 1985). They typically range over large territories that include heterogeneous habitats and landscapes (Newton 1979; Janes 1985; Watson 1997; Pedrini and Sergio 2002; Martínez et al. 2003; Sergio et al. 2003). Macrohabitat characteristics (vegetation types, topography, human pressure, availability of prey, etc.) are important components in breeding habitat selection (Janes 1985; Mosher et al. 1987; Bosakowski and Speiser 1994; Stern 1998; McGrady et al. 2002a, b; Sergio et al. 2004). This is especially important in species with very large home ranges, such as the golden eagle (Watson 1997), the species considered in this study.

The species

The golden eagle is a cosmopolitan species, distributed throughout the Northern Hemisphere (Del Hoyo et al. 1994; Watson 1997). In the Iberian Peninsula it mainly occupies mountainous areas and shows a preference for open landscapes such as montane grassland, rocky habitats and Mediterranean shrubland, avoiding heavily forested areas (Cramp and Simmons 1980; Tucker and Evans 1997; Arroyo 2003). Selection of breeding areas depends so much on the presence of appropriate cliffs, as well as adequate prey availability and low human pressure (Watson 1997).

In Europe, although some populations are stable or increasing locally (Haller and Sackl 1997), the golden eagle is considered scarce, with population decline in most countries. In Spain it is currently considered as Near Threatened species (Arroyo 2003). The main threats are associated with the human activities of hunting and poisoning, especially in areas where livestock are present (Cramp and Simmons 1980; Haller and Sackl 1997; Watson 1997; Bechard and McGrady 2002; Whitfield et al. 2004a, b). Populations in the Iberian Peninsula decreased in the 1970s but at present they seem to be stable (Díaz et al. 1996; Arroyo 2003), and indeed these populations are among the most important in the Western Palearctic (Del Hoyo et al. 1994; Birdlife International/European Bird Census Council 2000). In the region of Galicia (NW Spain) it is very scarce: the individuals present make up only about 0.4% of the Spanish population (Arroyo 2003), and it is restricted to the south-east, in the province of Ourense (Guitián et al. 1991; Arroyo, 2003; Martínez et al. 2003) (Fig. 1).

Many studies of the golden eagle have focused on relationships between population size and prey abundance, weather and habitat characteristics, both in North America (e.g. Marzluff et al. 1997; Steenhof et al. 1997; McIntyre 2002) and in Europe (Tjernberg 1984; Watson and Dennis 1992; Pedrini and Sergio 2001, 2002; McGrady et al. 2002a). Studies carried out in the Iberian Peninsula have focused either on the microhabitat characteristics of nesting cliffs or on broader macrohabitat characteristics; most such studies have been carried out in areas of relatively

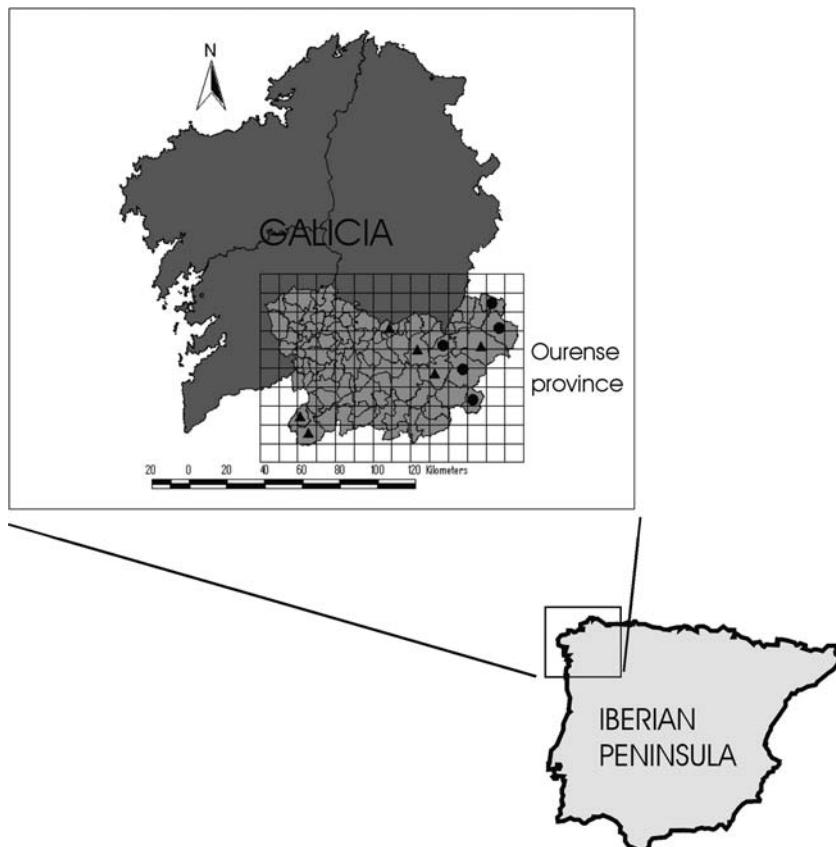


Fig. 1 Map of the study area in northwestern Iberian Peninsula, showing municipalities of the province of Ourense (the southeasternmost province of the four provinces of the region of Galicia) and current (●) and old (▲) nest sites of the golden eagle in this province

high golden eagle population density, and mainly in Mediterranean habitats (Fernández 1986; Donázar et al. 1989; Fernández 1993; Sánchez-Zapata and Calvo 1999; Carrete et al. 2000; Rico-Alcázar et al. 2001; among others). In northwestern Iberia the information available on habitat preferences is more limited, and mainly related to certain descriptive aspects of the nesting cliffs (Pimenta, 1980; Arroyo et al. 1990; Romero et al. 1995).

In this paper, we analyse both the historical and the present situation of the golden eagle in the province of Ourense, where it is present with low population density. Specifically, we used logistic regression procedures to identify those habitat variables that best predict the distribution of current and historical (1960s/70s) nesting sites, with the aim of generating maps of the potential distribution of the golden eagle in this region. We discuss conservation problems associated with food and nesting site availability, and with changes in land use and human disturbance that can affect habitat carrying capacity. We also propose management actions aimed at augmenting the golden eagle population in this region.

Methods

Study area

The province of Ourense ($41^{\circ}48' - 42^{\circ}35' N$, $6^{\circ}45' - 8^{\circ}21' W$) is located in the southeast of Galicia (NW Spain), with a total area of 7,278 km². It lies across the transition between the Atlantic and Mediterranean climates. Average annual rainfall ranges between 700 and 1,900 mm, and mean temperature between 8 and 16°C (Martínez-Cortizas and Pérez-Alberti 1999). Maximum altitudes are in the eastern zone (up to 2,100 m.s.l.), with minimum altitudes in river valleys. The geology is mainly dominated by highly fissured granitic rocks, shales and schists (Macias and Calvo 2001) so that craggy landscape features are common. The hydrographic network is constituted by the Miño-Sil system, and the Limia and Duero basins, which in several areas form pronounced river canyons. The natural vegetation is basically Eurosiberian in the central and western mountains, and Mediterranean in the rest of the province (Izco 1987). Natural woodland is characterized by *Quercus pyrenaica* and *Q. robur*, although chestnut forests are also present (*Castanea sativa*). A large part of the territory is dedicated to timber production, mainly *Pinus pinaster* and *P. sylvestris*. In the Atlantic region the dominant shrubland vegetation is gorse (*Ulex* sp.), while in the Mediterranean areas *Erica australis*, *Calluna vulgaris*, *Pterospartum tridentatum* and *Cistus ladanifer* are the most representative species, with mountainous zones dominated by *Cytisus* sp. and *Genista* sp. Over a large part of the province, traditional extensive land-uses are common, although gradually these are being abandoned and land is being recolonized by natural vegetation. The total population of the province is about 360,000 inhabitants (49 inhabitants/km²), mainly located in highly dispersed rural settlements. Wildfires, inadequate forestry practices, road infrastructures, mining, agriculture and livestock intensification are among the most important environmental problems (Pino 1992; Villarino et al. 2002).

Nest sites

To detect the presence of breeding territories during each spring from 1997 to 2002, we monitored different mountainous areas of Ourense with appropriate habitat for the nesting of this species. We also considered the available published information, mainly to establish historical breeding territories (López and Guitián 1983; Guitián et al. 1991; Romero et al. 1995; S.G.H.N. 1995; Arroyo 2003; Martínez et al. 2003; Ornithological yearbooks of Galicia 1993–2001), as well as field data provided by biologists, ecologists, other technical personnel and gamekeepers employed by the Galician regional government (Xunta of Galicia). The final prospected areas were the southwestern and southern mountains over the period 1997–2000, and the central and eastern mountains together with the river canyons over the period 2001–2002.

Habitat selection models and data analysis

Several environmental variables were selected to model habitat attributes, namely land use, degree of humanization, topographic irregularity, and habitat heterogeneity (Table 1). These parameters were represented on a 10×10 km grid using percentage, maximum, minimum or count values. This grid resolution is habitual in raptor studies (Watson et al. 1992; Sánchez-Zapata 1999; Carrete et al. 2000;

Table 1 Independent variables included in the logistic regression models

| Label | Description of the variable |
|--------------------------------------|--------------------------------------------------|
| No. settlements | Number of human settlements |
| Area of settlements | Area of human settlements |
| Road length (m) | Length of paved roads |
| Min. altitude (m) | Minimum altitude |
| Max altitude (m) | Maximum altitude |
| Max–min altitude (m) | Maximum altitude–Minimum altitude |
| Mean altitude (m) | Average altitude |
| Min slope (degrees) | Minimum slope |
| Max slope (degrees) | Maximum slope |
| Max–min slope (degrees) | Maximum slope–Minimum slope |
| Mean slope (degrees) | Average slope |
| Scrub–pasture area (km^2) | Area of scrubland and pastureland |
| Forest area (km^2) | Area of forest |
| Reservoir area (km^2) | Area of reservoirs (dammed water bodies) |
| Scrub–forest length (m) | Length of border between scrubland and forest |
| Scrub–reservoir length (m) | Length of border between scrubland and reservoir |
| Forest–reservoir length (m) | Length of border between forests and reservoir |

Sergio et al. 2004), and we considered it appropriate for representing the presence, home ranges and hunting movements of golden eagle, in relation to environmental characteristics. Radiotracking studies in other regions have shown that most of golden eagle movements occur within 6 km of the centre of their territory (Watson 1997; McGrady et al. 2002a).

Values for these environmental variables were obtained from 1:50,000 digital cartography with the aid of Geographic Information System software (GIS-ArcView 3.1.; Environmental Systems Research Institute, Inc., Redlands, CA). Continuous topographic variables (i.e., slope and altitude) were derived from a Digital Elevation Model with a resolution of 250×250 m. The remaining variables were obtained with the GIS using vectorial data. Scrubland, crops and pasture areas were identified using data from the CORINE Land Cover Project (EEA 1994). These vegetation types are often intermixed and not readily distinguishable at the spatial resolution used, so they were treated as the same vegetation type. All forest ecosystems were also treated as the same type, independently of their tree species composition. Forest information was obtained from the Third National Forest Inventory (D.G.C.N. 2000).

Modelling of the distribution of the golden eagle was done considering three different periods: (i) nesting areas in the period 1997–2002; (ii) old nesting areas (well-known nesting areas in the 1960s and 1970s); and (iii) current and old nesting areas pooled together. To establish areas with current or old nests and to integrate them into the analyses of habitat selection, the following approach was employed: first we identified municipalities in which there was some record of the presence of current and/or old nests; we then considered golden eagle to be present in those 10×10 km grid cells including at least 25% of the area of a municipality having a verified nest (Figure 1). Due to important changes in land use over the last 25–30 years in Ourense (Precedo 1995), the habitat selection analysis for old nesting areas was carried out without the variables related to land use, habitat heterogeneity and length of paved roads, since we considered that these variables have probably varied over this period; so for this analysis we used only topographic parameters and those related to human settlements.

Stepwise logistic regression analysis (Quinn and Keough 2002) was then performed with presence/absence of golden eagle as dependent variable, and the variables listed in Table 1 as independent variables. The analytical expression of the logistic function is $P = e^y / (1 + e^y)$ or $1/(1 + e^{-y})$ where P is the probability of the presence of the species, and y is a function of the type— $(k + ax_1 + ax_2 + \dots + zx_n)$, x_1, x_2, \dots, x_n being the selected independent variables. The significance of each variable included in the final regression model was determined by the Wald test (Quinn and Keough 2002). For all models obtained we calculated chi-square values (χ^2) (Hosmer and Lemeshow's test) describing the fit of the model to the logistic curve, and the associated significance level. Nagelkerke's test (R^2) was used as a test of goodness-of-fit. All analyses were performed using the statistical package SPSS v11.0 (McGraw-Hill, Madrid, Spain), taking $P < 0.05$ to indicate statistical significance.

With the aim of developing a higher-resolution approach for identifying current nesting areas, the best model was selected in two different ways:

1. Using classic logistic regression (saturated model, i.e. including all the variables in the analysis).
2. Using the Akaike Information Criterion (AIC) (Anderson et al. 2000):

$$\text{AICc} = -2 \log \text{ Likelihood } + 2K + \frac{2K(K+1)}{(n-K-1)}$$

where K is the number of parameters and n is the sample size (Burnham and Anderson 1998). This expression of AIC was used because $n/K < 40$ (Anderson et al. 2000). For each model i the values of AIC and Δ_i were obtained, where $\Delta_i = \text{AIC}_i - \text{AIC}_{\text{minimum model}}$, and the weight of each model was calculated as Wi :

$$Wi = \frac{\exp(-\frac{1}{2}\Delta_i)}{\sum_{r=1}^R \exp(-\frac{1}{2}\Delta_r)} \quad (\text{Anderson et al. 2000})$$

The sum of all weights equals to the unit, and the value of each Wi indicates the model i is the best overall Kulback–Leibler model (Anderson et al. 2000). Using the Akaike Information Criterion, no model is the null model, nor is a significance level established a priori. The best overall model is chosen from a group of well-defined candidate models (hypothesis) with biological meaning (Anderson et al. 2000; Seoane and Bustamante 2001). The importance of each independent variable is obtained by adding the Akaike weights to the models in which that variable is present (Burnham and Anderson 1998). The addition of the weights of each variable was considered consequential when $\sum Wi > 0.5$ (Taylor and Knight 2003). The candidate models were the result of the consideration of three individual environmental variables (maximum altitude, average slope and shrub-pasture area), the resulting combinations and interactions, giving a total of 10 models.

With the logistic models obtained for the different periods, the available habitat in the whole province of Ourense was evaluated using Geographic Information System software (GIS-ArcView 3.1) in order to generate maps of potential distribution. The cartographic models obtained showed estimated probability of occurrence within each 10×10 km grid square.

It was assumed that the distribution of the golden eagle in Ourense is known with full precision, with no false absences (Hirzel et al. 2002; Bustamante and Seoane 2004).

Results

Presence and population density of the golden eagle

At present (1997–2002) golden eagle breeding pairs in Galicia are located exclusively in the province of Ourense (Fig. 1). The population is thought to be 5 pairs, occupying a total area of 2,000 km² (average density of 1 pair/400 km²).

Over the last 30 years, the population of golden eagle seems to have remained constant in Galicia. In the 1970s, 4–6 pairs were estimated to have been present in the region, and this figure seemingly remained constant throughout 1980s. The existing data on the presence of individuals outside these breeding areas (Ornithological Yearbooks of Galicia, 1993–2001), almost certainly correspond to individuals in postbreeding dispersion or to individuals nesting in neighbouring territories of other regions.

Patterns of habitat selection

Habitat selection in current nesting areas

The final model obtained for predicting current nesting areas included only maximum altitude (Table 2), with a positive regression coefficient: $Y = 6.666 - 0.004 \text{ Max altitude}$ (Hosmer and Lemeshow test, $\chi^2 = 9.51, P = 0.301$). The overall correct prediction was 84.2%, explaining 32% of the variance. The most parsimonious model obtained using Akaike information criteria included maximum altitude (Table 3), although the models including Mean slope + Scrub–pasture area and Max altitude × Mean slope can also be considered competent ($\Delta_i < 2$). Of the predictive variables used, maximum altitude and average slope can be considered consequential (Table 4).

Habitat selection in old nesting areas (1960s and 1970s)

(A) Modelling using all environmental variables

The final model obtained includes maximum altitudinal range (maximum altitude–minimum altitude), average altitude, maximum slope range (maximum slope–

Table 2 Classic logistic regression model for the probability of breeding presence of the golden eagle in Ourense province, using current nesting areas on a 10 × 10 km grid

| | B | SE | Wald | P |
|--------------------|---------|-------|--------|-------|
| Interception value | - 6.666 | 1.426 | 21.838 | 0.000 |
| Max altitude | 0.004 | 0.001 | 14.995 | 0.000 |

Table 3 Logistic models for the probability of breeding presence of the golden eagle in Ourense province, using current nesting areas on a 10 × 10 km grid, showing Akaike information criterion values

| Model | R^2 | K | AIC | Δ_i | Wi |
|------------------------------------------------|-------|---|-------|------------|-------|
| Max altitude | 0.32 | 3 | 73.6 | 0 | 0.336 |
| Mean slope + Scrub–pasture area | 0.33 | 4 | 75.1 | 1.5 | 0.159 |
| Max altitude × Mean slope | 0.33 | 4 | 75.1 | 1.5 | 0.159 |
| Max altitude + Mean slope | 0.32 | 4 | 75.77 | 2.17 | 0.114 |
| Max altitude + Scrub–pasture area | 0.32 | 4 | 75.77 | 2.17 | 0.114 |
| Mean slope × Scrub–pasture area | 0.30 | 4 | 77.47 | 3.87 | 0.049 |
| Max altitude + Mean slope + Scrub–pasture area | 0.32 | 5 | 77.99 | 4.39 | 0.037 |
| Mean slope | 0.24 | 3 | 78.96 | 5.36 | 0.023 |
| Max altitude × Scrub–pasture area | 0.25 | 4 | 80.99 | 7.39 | 0.008 |
| Scrub–pasture area | 0.10 | 3 | 88.22 | 14.62 | 0.000 |

Table 4 Relative importances of effect magnitudes (calculated by adding for each variable the Akaike weights for all models) of the predictive variables used for the modelling the presence/absence of the golden eagle in Ourense province (analysis based on current nesting sites)

| Predictor | Relative importance | | |
|------------------|---------------------|------------------|--------------------|
| | Max. Altitude | Mean slope | Scrub–pasture area |
| Presence/absence | 0.76904 + | 0.54099 + | 0.37748 + |

In bold, values over 0.5 considered as consequential

minimum slope) and length of border between scrubs and reservoirs. All these variables contributed to the model with positive sign (Table 5): $Y = 13.824 - 0.007$ [Max.–min altitude] – 0.004 [Mean altitude] – 0.098 [Max–min slope] – 0.0002 [Scrub–reservoir edge] (Hosmer and Lemeshow's test, $\chi^2 = 7.04$, $P = 0.532$). The overall correct prediction was 72.3%, explaining 69.9% of the variance (Nagelkerke's $R^2 = 0.699$).

(B) Modelling using only variables unchanged over the last 25–30 years.

The final model obtained for old nesting areas included maximum altitudinal range, average altitude and maximum slope range, all with positive signs (Table 6): $Y = 12.12 - 0.006$ [Max.–min altitude] – 0.003 [Mean altitude] – 0.091 [Max–min slope] (Hosmer and Lemeshow's test, $\chi^2 = 7.52$; $P = 0.482$). The overall correct prediction was 72.3%, explaining 63.4% of the variance (Nagelkerke's $R^2 = 0.634$).

Table 5 Classic logistic regression model for the probability of breeding presence of the golden eagle in Ourense province, using old nesting areas on a 10 × 10 km grid

| | B | SE | Wald | P |
|----------------------|---------|-------|--------|-------|
| Interception value | –13.824 | 3.139 | 19.394 | 0.000 |
| Max.–min altitude | 0.007 | 0.002 | 10.762 | 0.001 |
| Mean altitude | 0.004 | 0.001 | 8.003 | 0.005 |
| Max–min slope | 0.098 | 0.051 | 3.713 | 0.054 |
| Scrub–reservoir edge | 0.0002 | 0.000 | 4.438 | 0.035 |

Table 6 Classic logistic regression model for the probability of breeding presence of the golden eagle in Ourense province using old nesting areas on a 10 × 10 km grid, and considering only variables that have remained unchanged over the last 25–30 years

| | B | SE | Wald | P |
|--------------------|----------|-------|--------|-------|
| Interception value | – 12.126 | 2.647 | 20.992 | 0.000 |
| Max.–min altitude | 0.006 | 0.002 | 10.18 | 0.001 |
| Mean altitude | 0.003 | 0.001 | 8.236 | 0.004 |
| Max–min slope | 0.091 | 0.048 | 3.604 | 0.058 |

Habitat selection in both current and old nesting areas

The final model obtained using both current and old nesting areas included maximum altitude, average slope and scrub–pasture areas, all with positive signs (Table 7): $Y = 11.805 – 0.003$ [Max altitude] – 0.471 [Mean slope] – 6.01×10^{-8} [Scrub–pasture area] (Hosmer and Lemeshow's test, $\chi^2 = 13.38$; $P = 0.099$). The overall correct prediction was 68.3%, explaining 67.7% of the variance (Nagelkerke's $R^2 = 0.677$).

Summarizing, the logistic regression analyses carried out for these three different data sets selected a total of 7 environmental variables, all with positive sign. In two cases maximum altitude was included, while maximum altitudinal range, average altitude, maximum slope range, average slope, scrub–pasture area and the length of scrub–reservoir were each included only in one case.

Two areas were identified as potentially appropriate for the golden eagle, in the eastern and southwestern sectors of the province. The probabilities of occurrence predicted by the models suggest that habitat availability is lower in the models computed for current nesting areas (Fig. 2) than in those taking into account old nesting areas or a combination of current and old nesting areas (Figs. 3 and 4).

Discussion

Given the environmental characteristics of this region, the Galician population of golden eagle was probably never very numerous.

This population may have reached its minimum level at the end of 80s under the sustained effects of poisoning and hunting (Gutián et al. 1991; Romero et al. 1995; Tapia 2004). Since then, however, legislative and social changes have led to the almost complete eradication of poisoning, which together with increasing land abandonment (i.e. less human pressure) may be the major factor explaining the recovery of golden eagle still apparent today. Poisoning, however, persists to a

Table 7 Classic logistic regression model for the probability of breeding presence of the golden eagle in Ourense province, using current and old nesting areas on a 10 × 10 km grid

| | B | SE | Wald | P |
|--------------------|-----------------------|-------|--------|-------|
| Interception value | – 11.805 | 2.370 | 24.821 | 0.000 |
| Max altitude | 0.003 | 0.001 | 7.018 | 0.008 |
| Mean slope | 0.471 | 0.148 | 10.133 | 0.001 |
| Scrub–pasture area | 6.01×10^{-8} | 0.000 | 9.746 | 0.002 |

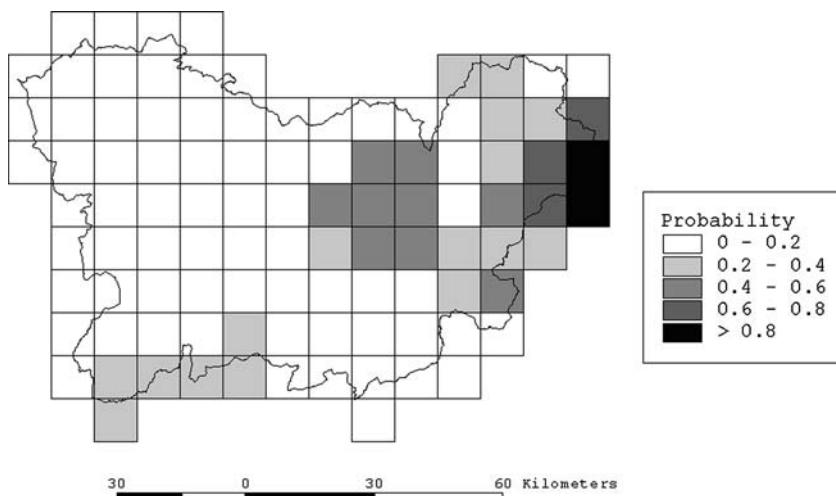


Fig. 2 Probability of occurrence of golden eagle in the study area according to the logistic model obtained with current nesting areas using the Akaike information criterion

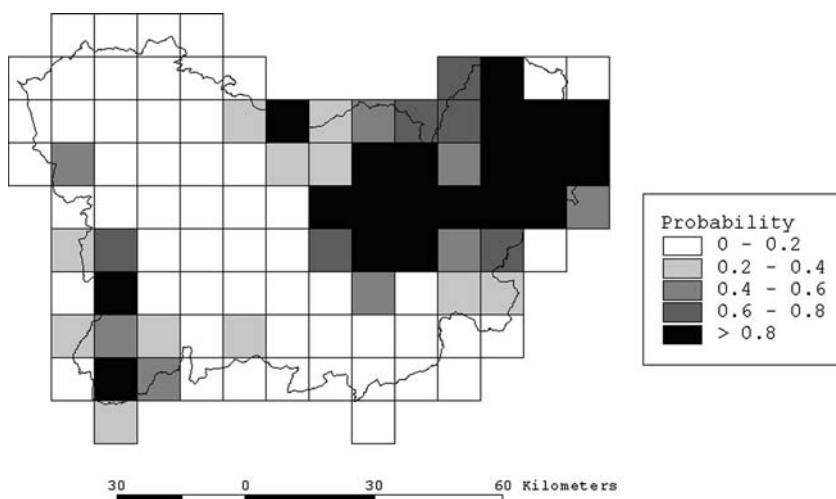


Fig. 3 Probability of occurrence of golden eagle in the study area according to the logistic model obtained with the old nesting areas using all the environmental variables

certain extent in Spain (Hernández 2001), and its possible effects must be monitored, because non natural mortality acting on a small, fragmented and seemingly isolated population could have strong deleterious population effects.

Models of habitat selection and conservation problems

At the spatial resolution considered breeding areas showed a close association with extensive mountainous areas, as occurs in other area of the Iberian Peninsula (Carrete et al. 2000). In areas of low golden eagle population density, such as northwest Iberia, nesting sites are scarce, constituting a limiting factor

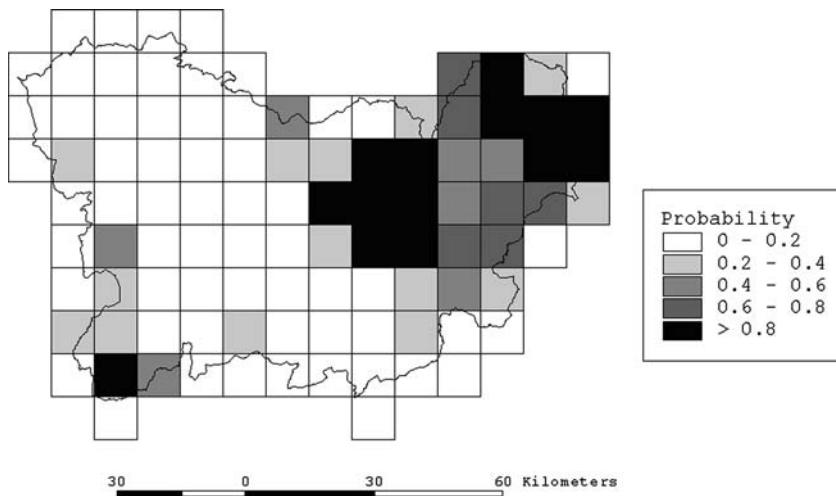


Fig. 4 Probability of occurrence of golden eagle in the study area according to the logistic model obtained with the current and old nesting areas

(Heredia et al. 1988). All golden eagle pairs currently present in Galicia are cliff-nesting (Romero et al. 1995), and thus presence of cliffs must be a decisive factor determining the presence and population density of this species in this region.

The traditional smallholding land ownership in Ourense, and our consideration only land uses (scrub–pasture area and forest area), probably explain the fact that we did not detect negative relationships between golden eagle distribution and intensive agricultural uses. Such negative relationships have been reported for this species and other raptors in Iberia and other parts of Eurasia (Marquiss et al. 1985; Tella et al. 1998; Sánchez-Zapata 1999; Carrete et al. 2000; Carrete et al. 2002; Sánchez-Zapata et al. 2003). Taking into account that traditional non-intensive agriculture systems are a fundamental component in ecosystem conservation in the Iberian Peninsula (Tucker and Evans 1997; Tella et al. 1998; Carrete and Donázar, 2005), the modification and revision of the current CAP (Common Agricultural Policy) is a key requirement from the conservation point of view (De la Concha 2002; Villarino et al. 2002).

The presence of the scrub–pasture area variable in one of the competent models for predicting current nesting area, although not as a consequential variable, suggests the importance of this habitat for the golden eagle population. It has been shown in other European regions that golden eagles do not avoid forest, especially if trees are spaced out (Carrete et al. 2000; Watson 1997), but the negative effects of afforestation of large areas of shrubland have been clearly demonstrated (Watson 1992; Whitfield et al. 2001). These negative effects generally include a decrease in appropriate hunting areas, prey density, and consequently breeding success (McGrady et al. 1997; Watson 1997; Pedrini and Sergio 2001; Whitfield et al. 2001; McGrady et al. 2002a). Food availability explains most of the variation in raptor population density, except where nest site availability is limiting (Newton 1979; Steenhof et al. 1997; Watson 1997; Pedrini and Sergio 2002), as seems likely in the study area. Open shrubland areas are positively selected by the golden eagle as hunting habitats, because the vegetation structure favours prey detection and

hunting success (Marzluff et al. 1997; Balbontín, 2005; Ontiveros et al. 2005). Moreover, these habitats often have the highest densities of the major prey species (Iberian hare, European wild rabbit and Red-legged partridge) (Palomares and Delibes 1997; Sánchez-Zapata 1999).

Carrion feeding by the golden eagle is frequent when natural prey is scarce (Watson 1997; Gómez 2001). In many areas of Europe this species lives in free-range areas of livestock farming (Donázar et al. 1996; Watson 1997). In these situations, land-use changes may cause a reduction in food availability and, consequently, a decrease in breeding success and/or population densities. The decrease in extensive livestock in Ourense over the last 30 years and the progressive abandonment of rural areas (Precedo 1995) may have limited the availability of carrion, especially important for the survival of young individuals (Zocchi and Panella 1996; Watson 1997). Paradoxically, in spite of the benefits of extensive pasture, extensive livestock was usually linked to an indiscriminate use of poisons, which possibly contributed in the decline of the Galician golden eagle population in the 1970s and 1980s.

In the model obtained with the old nesting areas, the inclusion of length of scrub–reservoir border as a predictor variable reflects the anthropophobic breeding behaviour of this species (Watson 1997; Petty 1998; McGrady et al. 2002b): it avoids settlements and uses river canyons, here indicated by scrub–reservoir border length, for breeding.

Although golden eagle density in Ourense is very low, the cartographic models obtained from old nesting areas and from a combination of old and current nesting areas suggest that the potentially available habitat is sufficient for a larger number of breeding pairs.

Management implications

Conservation measures based only on the protection of nesting areas have been considered habitually inadequate for large raptors, and the protection and management of larger areas has been proposed as a more effective conservation tool (Widen 1994; Tucker and Evans 1997; Pedrini and Sergio 2002; Carrete and Donázar 2005; Whitfield et al. 2006). In this connection, the areas in Ourense identified by our cartographic models as important for the golden eagle are included in the Natura 2000 Network, but their conservation management is still very deficient.

The GIS-based model presented here could be used by managers: (1) to simulate the effects of silviculture, mining or fires, thus allowing for effective assessment of environmental impacts (Madders and Walker 2002; Martínez et al. 2003); (2) to manage shrublands in order to enhance prey density and prey detection (Ontiveros et al. 2005); (3) to annually identify areas in which to monitor the presence of poison, hunting and interactions with wind farms and power lines; (4) to regulate outdoor recreation activities potentially hazardous for golden eagles (Liddle, 1997); (5) and to catalogue the cliffs and rocky outcrops potentially suitable for nesting. In Ourense, the breeding territories currently contain several nests (Martínez et al. 2003) and their conservation is a high priority, because enables the eagles to diminish the human pressure changing the nest (Álvarez and Díaz 1997). Information about the location of nesting areas must be updated annually to allow the generation of new models of suitable areas, to predict range expansions or identify suitable locations for reintroductions, and also to provide a basis for design of protected areas (McLeod et al. 2002, O’toole et al. 2002; Balbontín 2005).

Finally, it should be noted that the monitoring of breeding productivity, knowledge of age classes, measures of survival and Population's Viability Analysis (PVA) are all very useful conservation tools (see Real et al. 1991; Real and Mañosa 1997; Hunt 1998; Beeisinger and McCullough 2002; Whitfield et al. 2004a, 2006).

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The arctic fox *Alopex lagopus* in Fennoscandia: a victim of human-induced changes in interspecific competition and predation?

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Abstract After a marked decline at the beginning of the 1900s, the arctic fox *Alopex lagopus* population in Fennoscandia has remained at a very low level. We suggest that the main cause for the population crash was winter starvation caused by (1) over-hunting of reindeer *Rangifer tarandus* populations, and thus reduced carcass availability in the mountains, and (2) increased interspecific competition for these carcasses because of increased invasion of red foxes *Vulpes vulpes* from lower altitudes. The failure of arctic fox populations to recover, despite increasing reindeer populations in the mid 1900s, can be explained by a concurrent strong increase in red fox numbers. Analyses of countywide hunting statistics from Norway 1891–1920 suggest that there actually was an increase in red fox numbers in the period of arctic fox decline, and that the increase in reindeer populations from the 1920s to the 1950s was accompanied by a new increase in red fox numbers. We conclude that restoring arctic fox populations most likely will require a substantial and lasting reduction of red fox populations.

Keywords Arctic fox · Cervid carcasses · Interspecific competition · Norway · Small rodents · Snow depth

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Introduction

With an estimated population size of less than 200 adult individuals at the end of the 1900s the arctic fox *Alopex lagopus* is now regarded as the most endangered mammal species in Fennoscandia (Linnell et al. 1999a), but conservation strategies suffer from the lack of a commonly accepted diagnosis (e.g. Hersteinsson et al. 1989; Hersteinsson and Macdonald 1992; Angerbjörn et al. 1995; Kaikusalo and Angerbjörn 1995; Löfgren and Angerbjörn 1997; Linnell et al. 1999b). Hundred years ago, the arctic fox was common in most Norwegian mountains, and Collett (1912) assumed that approximately 2000 arctic foxes were hunted annually during 1879–1911. At the end of this period, there was a sudden decline (Johnsen 1929; Høst 1935; Linnell et al. 1999b), and despite 65–75 years of protection, and an unusually high reproductive capacity (Tannerfeldt and Angerbjörn 1998), the Fennoscandian arctic fox populations never recovered.

Hersteinsson and Macdonald (1992) suggested that the geographical distribution of arctic foxes are limited to the south by interspecific competition with the larger red fox *Vulpes vulpes*, whereas red foxes are limited to the north by resource availability. This raises the possibility that the main cause for the arctic fox decline was not over-hunting, as commonly assumed (Curry-Lindahl 1965; Hersteinsson et al. 1989; Kaikusalo and Angerbjörn 1995; Loison et al. 2001), but rather increased competition or even predation (Frafjord et al. 1989) from increasing red fox populations (Johnsen 1929; Hjeljord 1980).

The survival and reproduction of both fox species probably varies with winter food conditions, especially at higher altitudes and latitudes. A negative relationship between hunting records of red foxes in Norway and snow depth in the previous winter (Selås and Vik 2006) indicates that deep snow, which makes small rodents less available (Lindström and Hörfeldt 1994), reduces fox survival and reproduction. Under such conditions, ungulate carcasses are probably of vital importance for foxes (e.g. Jedrzejewska and Jedrzejewski 1998). Possibly as a result of the eradication of wolf *Canis lupus* and other large predators in Norway (Johnsen 1929), the lowland cervid species moose *Alces alces* and red deer *Cervus elaphus* expanded in range and abundance from the late 1890s (Jacobsen and Andersen 1990; Langvatn 1990). The mountain-dwelling reindeer *Rangifer tarandus*, in contrary, declined dramatically in the 1800s (Skoglund 1990), probably due to the advent of modern rifles and the absence of hunting restrictions before 1899.

We hypothesise that: (1) The decline of the arctic fox in Fennoscandia in the early 1900s was caused mainly by increased winter starvation, due to a decrease in the supply of reindeer carcasses and increased competition for carcasses from an expanding red fox population. (2) The arctic fox has been unable to benefit from the increased abundance of reindeer in the mid 1900s because of further expansion by the red fox. Here, we use Norwegian hunting statistics to demonstrate the likelihood of an increase in red fox populations both during the period of arctic fox decline and during the period of reindeer increase.

Methods

Hunting statistics provide a countywide survey of the annual number of bounties paid for foxes from 1880 to 1976 (Central Bureau of Statistics of Norway 1978). We divided

the counties in South-Norway into six regions when presenting the hunting statistics; South-west = Rogaland and Hordaland Counties, south = Vest-Agder, Aust-Agder and Telemark Counties, east = Buskerud, Oppland and Hedmark Counties, south-east = Vestfold, Østfold and Akershus Counties, north-west = Sogn og Fjordane and Møre og Romsdal Counties, central = Sør-Trøndelag and Nord-Trøndelag Counties, north = Nordland and Troms Counties. In Finnmark, North-Norway, bounties were not paid for foxes in winter during 1910–1932, and therefore this county was omitted from the analyses. For economical and political reasons, few counties paid bounties during 1933–1945. Prior to this period, Johnsen (1929) assumed that trends in fox hunting statistics reflected trends in their population levels.

Unfortunately, arctic and red foxes were not distinguished in the statistics, but after the strong decrease in arctic fox numbers 1905–1910 (Johnsen 1929; Høst 1935), most bounties paid will refer to red foxes. To investigate whether there was a decline in arctic fox bounties and an increase in red fox bounties during 1891–1920, when arctic fox populations declined, we calculated the exponential growth rate of the number of bounties paid (the slope of the regression of $\ln N$ against time) for each of the 14 counties that had both arctic and red fox populations. We expected this growth rate to be negative in counties with a high proportion of arctic fox habitats and positive in counties dominated by red fox habitats. As indicators of relative habitat availability we used the proportion of land above the tree line (Tomter 1994) and latitude (measured midway between the northernmost and southernmost point in each county), because the arctic fox tolerates long winters better than the red fox.

To test whether the red fox populations in the mid 1900s responded not only to factors associated with main habitats in the lowland, but also to the growth in reindeer populations in the mountains, we calculated a population increase index for both red fox and reindeer for each county in South-Norway with reindeer hunting (data taken from Central Bureau of Statistics of Norway 1978). The indices were calculated as the average number killed per year in 1951–1960, divided by the average for 1921–1930. The three counties from North-Norway, with only domestic reindeer, were not used because also changes in reindeer management may have influenced the availability of carcasses in this region. Because of the relative small sample sizes and possible deviations from the normal distribution, we used non-parametric statistics (Siegel and Castellan 1988) when we compared fox indices with the selected explanatory variables.

Results

In all regions in South-Norway, the number of fox bounties paid increased with time from 1880 until about 1910 (Fig. 1). From then to about 1930, it remained fairly constant in the south-east region (Fig. 1), where red fox was the only fox species. Also in south and south-west, there were minor changes in this period, while there was a decline in the east, north-west and central regions (Fig. 1). In North-Norway, with the highest proportion of arctic foxes, the number of bounties fluctuated regularly prior to 1910, and thereafter declined markedly (Fig. 1).

During 1891–1920, the number of fox bounties showed a positive trend in all counties in South-Norway except Sør-Trøndelag and Sogn og Fjordane, whereas the trend was negative in both counties in North-Norway (Fig. 2). Fox growth rate (for

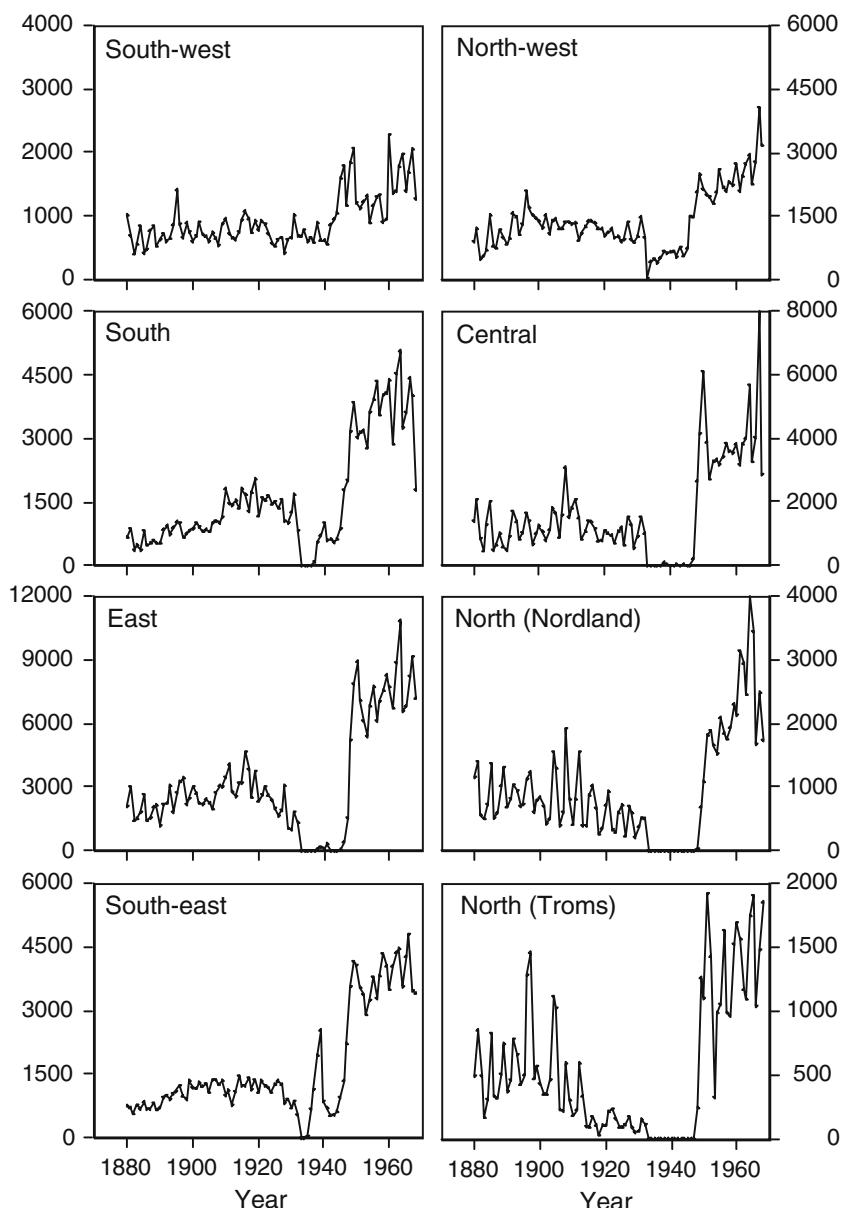


Fig. 1 Total number of bounties paid for foxes (red and arctic combined) in different regions of Norway. After 1910, most bounties refer to red fox, and after 1930, only red foxes were rewarded. In south-eastern Norway, red fox was the only fox species present. The strong decline in arctic fox populations in 1905–1910 is reflected mainly by the hunting statistic from Nordland and Troms, North-Norway. For economical and political reasons, few counties paid bounties for foxes during 1933–1945

both species combined) was negatively related to both latitude ($n = 14$, Kendall's Tau = -0.70 , $P < 0.001$) and the proportion of land above the tree line ($n = 14$, Kendall's Tau = -0.80 , $P = 0.003$). The relationship with the proportion of land

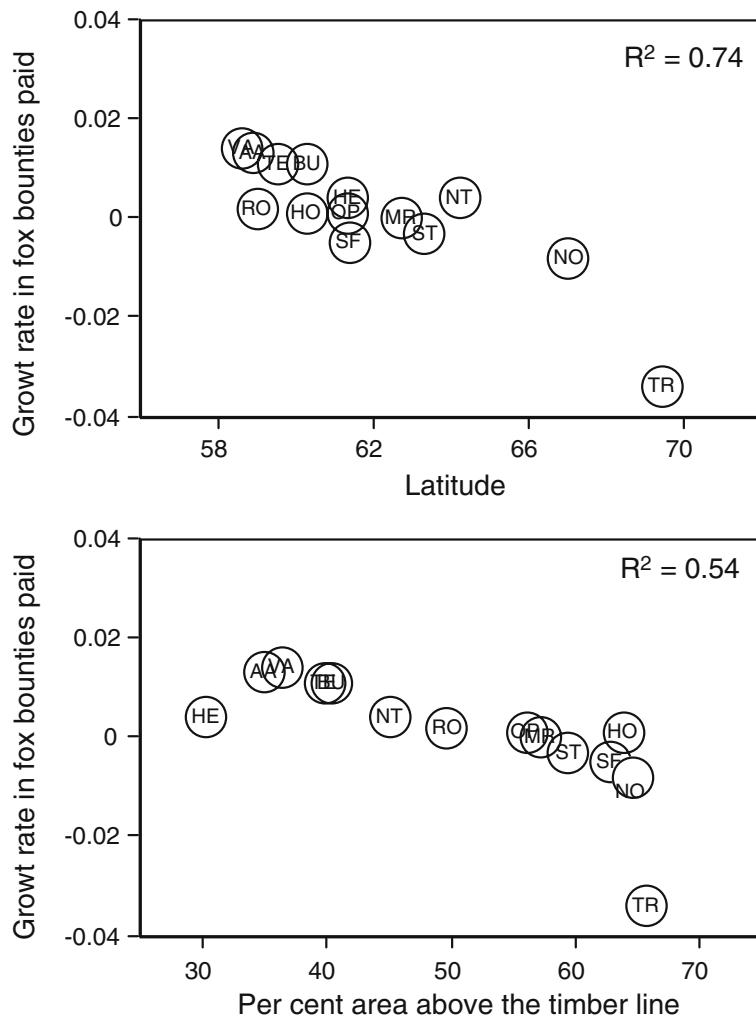


Fig. 2 The slope of the log-transformed regression curve for fox bounties (arctic and red combined) paid in each county during 1891–1920, in relation to the mean latitude and the proportion of area above the tree line in that county. For both figures, the ratio between red and arctic fox habitats decreases from the left to the right. The counties are Rogaland (RO), Hordaland (HO), Vest-Agder (VA), Aust-Agder (AA), Telemark (TE), Buskerud (BU), Oppland (OP), Hedmark (HE), Vestfold (VF), Østfold (ØF), Akershus (AK), Sogn og Fjordane (SF), Møre og Romsdal (MR), Sør-Trøndelag (ST), Nord-Trøndelag (NT), Nordland (NO) and Troms (TR)

above the tree line was highly significant also when latitude was controlled for ($n = 14$, Kendall's partial Tau = -72 , $P < 0.001$).

In all regions, the number of red fox bounties showed a marked increase from the 1920s to the 1950s (Fig. 1). The increase in reindeer populations in the mid 1900s, as reflected by the number of animals killed, coincided with the strong increase in red fox numbers, reflected by the number of bounties paid (Fig. 3). When using counties as statistical unit, there was a significant positive relationship between the population

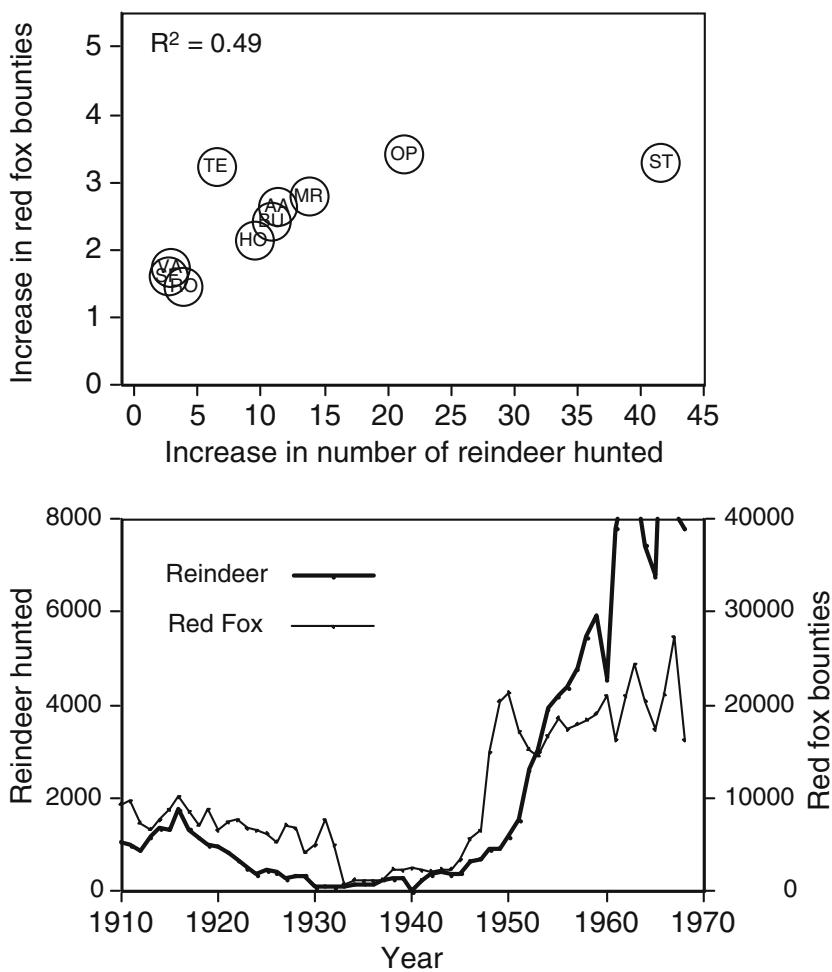


Fig. 3 Total number of wild reindeer and foxes (mainly red fox) killed in South-Norway 1910–1970, and the increase in fox bounties in each county from 1921–1930 to 1951–1960, compared with the increase in the number of reindeer hunted. County legends as in Fig. 2

growth index of red fox and reindeer from the 1920s to the 1950s ($n = 10$, Kendall's Tau = 0.69, $P = 0.006$; Fig. 3).

Discussion

There was a general increase in the number of bounties paid for foxes in Norway during 1880–1932. The regional pattern for the period 1891–1920, when the arctic fox population declined strongly, confirms that the increase was due to an increase in bounties paid for red foxes. Although the aim of the reward system was predator extermination, several game biologists concluded that the persecution had minor or no effects on red fox populations, which rather increased after the introduction of bounties in 1879 (Dahl 1927; Johnsen 1929; Lund 1963). We find the most likely

explanation for this increase to be increased supply of carcasses after the population growth of forest-living ungulate species, which may have benefited from the eradication of large predators (e.g. Okarma 1995; Boertje et al. 1996). The absence of large predators probably favoured the red fox also directly, through reduced predation risk at carcasses in winter (e.g. Jedrzejewska and Jedrzejewski 1998; Linnell et al. 1998).

Support for the view that increased red fox populations were detrimental for the arctic fox is that sterilised red foxes have successfully been used to eradicate arctic foxes from islands in Alaska (Bailey 1992). In Sweden, a combination of winter feeding and reduction of red fox populations has improved reproduction in the arctic fox (Angerbjörn et al. 2002). In Børgefjell (Nordland County), there were several years with good reproduction of arctic foxes during 1980–1998, probably because of a combination of winter feeding, high numbers of lemmings *Lemmus lemmus* and very low red fox populations due to an epizootic of sarcoptic mange (Frafjord et al. 1998).

Reindeer has constituted 30–45% of the winter diet of arctic foxes in the few studies made (Kaikusalo and Angerbjörn 1995; Strand et al. 1999; Frafjord 2000). Arctic foxes have bigger litters when small rodents are abundant (Angerbjörn et al. 1995, 1999; Strand et al. 1999), but supplemental feeding during winter may increase the proportion of reproducing foxes (Angerbjörn et al. 1991). In fact, arctic foxes have failed to reproduce in peak lemming years (Kaikusalo and Angerbjörn 1995), possibly because of poor body condition in spring.

There probably was an increase in the supply of reindeer carcasses in the mid 1900s, as a result of increased populations of wild reindeers (Skoglund 1990) and reduced inspection of domestic reindeers (Skjenneberg and Slagsvold 1968). This potential benefit for the arctic fox may, however, have been offset by a further increase in cervid and thus red fox populations in the lowland (Selås and Vik 2006), resulting in increased immigration of red foxes to the mountains. However, the positive correlation between the population growth indices of red fox and reindeer indicates that red foxes also responded directly to increased availability of reindeer carcasses in the mountains.

We conclude that the most likely cause for the population decline of the arctic fox in Fennoscandia was winter starvation caused by interspecific competition for reindeer carcasses. We also conclude that competition from red foxes is the most likely explanation for the lack of recovery of arctic fox. Hence, restoring arctic fox populations in Fennoscandia may require a substantial and lasting reduction of red fox populations. This conservation strategy should, however, be accompanied by extensive studies of interactions between the two fox species, in order to achieve better understanding of the impact of red foxes on arctic fox populations.

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Do biodiversity patterns in Dutch wetland complexes relate to variation in urbanisation, intensity of agricultural land use or fragmentation?

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Abstract Red list species densities of birds (maximally 22 km⁻²), and angiosperms (maximally 39 km⁻²) were used as biodiversity indicators in 21 larger complexes of wetlands across the Netherlands. Their covariability with a range of indicators of human land use was assessed, including population, road and visitor density, area covered by agriculture, open water, forest and residential housing. Data were collected on the wetland complexes as well as for a perimeter with 10 km radius. In a principal components analysis (PCA) with all land use variables, it was found that the population-density-related complex of urbanisation, fragmentation (by roads), and intensity of fertilizer use together explained most of the variability present (i.e. the first PCA axis explained 50%), whilst land use within these complexes was second with an additional 19% and waterside recreation third with 12%. Red list bird species density did not correlate with that of angiosperms, nor with any of the indicators used. For the 13 complexes on organic peatland, we observed an increase in maximum red list angiosperm species density with the proportion of open marshland ($P < 0.01$, $r^2 > 0.55$), which, in turn, was negatively and closely correlated with the first PCA axis reflecting an urbanisation gradient across the Netherlands.

Keywords Species richness · Indicators · Land use intensity gradient · Spatial pattern · Mires · Multivariate analysis

Introduction

Biodiversity of wetlands is considered to have substantial conservation (Cornwell and Grubb 2003) and economic value (Brander et al. 2006). It has been observed to decline due to a range of reasons generally linked to human activities (Wheeler 1988; Gibbs 2000; Balmford et al. 2002).

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Due to its particular geomorphology, the Netherlands abounds with wetlands (Verhoeven 1992). These wetlands have been subject to human exploitation for centuries, resulting in a highly anthropogenic landscape with spatial pattern governed by ditches and narrow elongate parcels of land since medieval reclamation in the 12th to 14th century. With the rise of adjacent towns such as Amsterdam in the 16th and 17th century, peat excavation has been carried out at large scales to satisfy the urban needs for fuel. This practice has often led to the formation of artificial lakes, where excessive excavation enabled erosion by winter storms.

In the 20th century these complexes of lakes, fens and carr were recognized as important areas for nature conservation (Barendregt et al. 1995). Most of these wetland complexes now harbour nature reserves as well as areas of intensive aquatic recreation (for example, several hundreds of boats pass the locks of the Loosdrechtse Plassen in a day; Vermaat and De Bruyne 1993), water quality is often poor (Van der Molen and Portielje 1999, Lamers et al. 2002), and roads, intensified agriculture and built-up area have fragmented these wetland habitats (Vos and Chardon 1998). The concerted impact of these pressures is thought to have led to a substantial decline in wetland biodiversity (Graveland 1998; Vereniging Natuurmonumenten 1998; Lamers et al. 2002). The relative importance, however, of these different pressures has not been addressed simultaneously so far, although negative effects of fragmentation and eutrophication on species richness are covered well in the literature (Phillips et al. 1978; Hough et al. 1989; Vos and Chardon 1989; Brose 2001; Verboom et al. 2001; Bailey et al. 2002; Blomqvist et al. 2003; Pellet et al. 2004). Our aim was to assess the relative importance of these different interacting factors. Our research questions were (1) does variability exist in biodiversity among these wetland complexes, and (2) does this present variation co-vary with contemporary patterns in human population density, intensity of agricultural land use, recreation or fragmentation. The database consists of contemporary data (~2000–2005), hence historically important determinants and past change cannot be inferred directly from observed patterns.

Materials and methods

We carried out a comparative multivariate analysis for 21 wetland complexes of substantial size (mean 20, range 0.4–62 km²). All these wetland areas had parts with a conservation status and parts with free access and a range of economic activities. We focused on identifiable landscape complexes of sufficient size, to overcome the well-established and potentially strong effect of small habitat size on species richness (e.g. Møller and Rørdam 1985; Brose 2001; Verboom et al. 2001). In addition to 13 peatland complexes, which were mires, fens or partly drowned bogs on organic peat soil (Table 1) two other types of common wetland landscapes were included: (a) coastal wetlands, generally with substantial areas of salt marsh ($n = 4$ complexes), (b) riverine, containing reed beds, backwaters and softwood forest ($n = 4$).

In our analysis biodiversity indicators would serve as dependent variables, and indicators of agricultural land use intensity, human population density with associated built-up land, recreation intensity and landscape fragmentation as independent explanatory variables. Past changes in either of these or other factors may well have affected biodiversity strongly, but have not been incorporated here. Principal

Table 1 Names, codes and areas of 21 studied wetland complexes as delimited in this study grouped into the types “coastal”, “riverine” and “fens or bogs”. Each entry has name of wetland, then in brackets code in Fig. 1 and area of the complex (km^2)

| Type | Wetland complex |
|------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Coastal | T Zwin (19–0.4), Verdronken land van Saeftinghe (20–29.5), Boschplaat (1–15.8), Zwanenwater (4–4.5) |
| Riverine | Biesbosch (18–46.9), Ooijpolder (17–3.0), Blauwe Kamer (16–1.3), Oostvaardersplassen (8–52.2) |
| Fen or bog | Vinkeveense Plassen (12–13.8), Reeuwijkse Plassen (15–10.9), Nieuwkoopse Plassen (14–15.9), Loosdrechtse Plassen (13–34.4), Kortenhoefse Plassen (11–3.1), Ankeveense Plassen (10–4.4), Naardermeer (9–6.3), Wieden (7–49.2), Weerribben (6–42.1), Rottige Meenthe (5–13.2), Fochteloer Veen (3–23.0), Alde Feanen (2–18.0), Worm, Jisp and Neck (21–27.1) |

component analysis (PCA), analysis of variance, bivariate and stepwise multiple linear regression were used as analytical tools.

Data were collected from the Netherlands Statistics Service (CBS 2005) and the freely accessible data depository of joint Dutch organisations for nature protection and natural history (Natuurloket 2004), and published literature (Table 2). The Natuurloket depository allows queries for numbers of individual red list species and related aggregate statistics for separate cells of the Dutch national km^2 -grid. Spatial extent and reliability of the data varies depending on availability, administrative units applied and effort made during the original collection (compiled in Table 2). Using arcGIS software, we delineated the individual complexes as separate spatial units on the digital land use map of The Netherlands (CBS 2000) primarily as

Table 2 Data sources and spatial resolution of variables used

| Variables used | Resolution | Data source |
|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|------------------------------------------------|--------------------------------------------------------|
| <i>Biodiversity indicator</i> | | |
| Number of red list bird and angiosperm species (mean, median, maximum, standard deviation) | Wetland complex, aggregated from km^2 | Natuurloket (2004) |
| <i>Within wetland complexes</i> | | |
| Visitor density, scaled to a per km^2 and per year basis | Wetland complex | Hein et al. (2005), Vereniging Natuurmonumenten (1998) |
| Percentage of marshland, agricultural land, forested land, open water, residential and recreational built-up land, road cover, also perimeter exact area of the wetland complex | Wetland complex, aggregated from km^2 | CBS (2000) |
| <i>Land use in perimeter of 20 km diameter</i> | | |
| Density of main and secondary roads (m km^{-2}), percentage of area residential and recreational | Perimeter | CBS (2000) |
| Nitrogen fertilizer use in 2002; population density | Municipality | CBS (2005) |

hydrologically homogeneous polder units and apparent geographically distinct entities in the surrounding landscape. This latter part has a subjective component and was therefore carried out by two people at the same time. In addition, a perimeter with radius of 10 km was delineated and a range of land use statistics were quantified (Table 1 and Fig. 1). The digital land use map distinguishes 38 types of

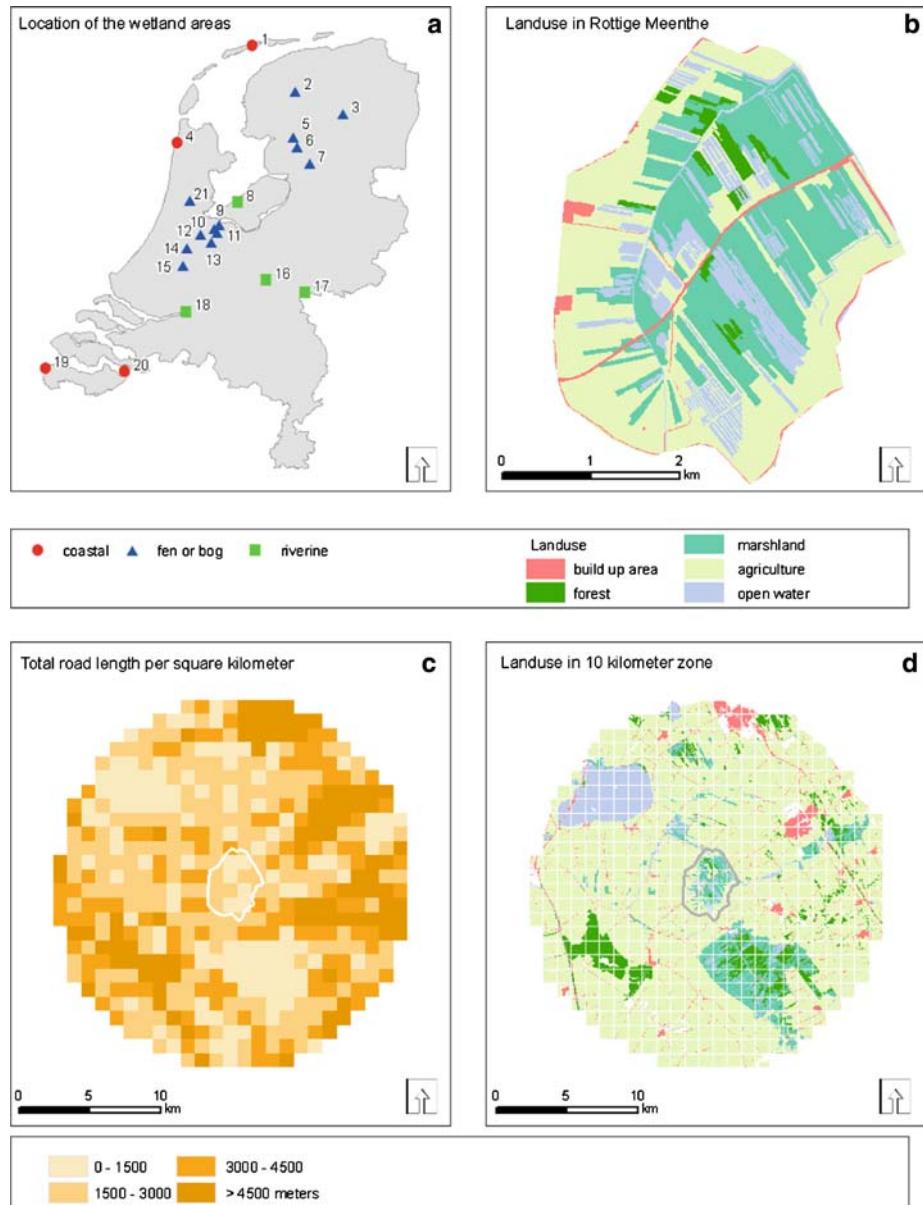


Fig. 1 (a) Location of the 21 wetland complexes across The Netherlands, (b) different types of land use in a sample wetland complex (Rottige Meenthe—area 5 in (a)), (c) delineation of the wetland complex in the surrounding perimeter, with road density indicated in a km^2 -grid, (d) land use in the surrounding perimeter

land cover including forest, marshland (wetland without trees, such as fens and reed beds), and open water.

Part of the data has been collected at a km^2 -resolution, but we use wetland complex as our basic replicate unit, since these can be considered as spatially sufficiently separate to reduce the degree of spatial dependence and pseudoreplication (Hurlbert 1984). This approach led to a variable grain (area of the complex) and an extent of about 50,000 km^2 (i.e. the whole of The Netherlands).

We limited ourselves to the occurrence of red list birds and angiosperm plants, since only these two biodiversity indicators had a satisfactory coverage of the km^2 grid across the country. Initially we included the species on both the red list as well as the alternative ‘Flora and Fauna’-list. We found however, that these two were correlated well ($r^2 = 0.65$, $P < 0.001$, $n = 308 \text{ km}^2$ units pooled over wetland complexes).

Results

The spatial gradient in population density across The Netherlands (Fig. 2a and Table 3) could be grasped well by the simple metric of travelling distance to Amsterdam, the capital, which was also correlated closely to estimated travelling time by car ($r^2 = 0.74$, $P = 0.001$). Distance from Amsterdam varied from 22 to 250 km for the wetland complexes studied (Table 3). A range of factors co-varied significantly with distance from Amsterdam, such as area of built-up land for residential or recreational purposes, road density in the wetland complex, visitor density, intensity of fertilizer use and proportion of open water in the complex (Fig. 2). The proportion covered by marshland increased with distance from Amsterdam (Fig. 2).

A principal component analysis (Table 3) revealed that half the variance in this multivariate dataset could be explained by a first component that reflects a complex of factors related to population density and urbanisation. Notably, the percentage of marshland correlated negatively to this component and agricultural fertilizer use did so positively. The second component related to agricultural land use within the wetland complex and explained 19% of the variance. The last component was correlated negatively to open water and visitor density, hence, may be interpreted as associated with recreation on water. It explained an additional 12%. When the same PCA was carried out for the peatland wetlands only, most patterns of significance remained identical to Table 3 and the overall explained variance of 86% was also comparable. Two exceptions were fertilizer application (no correlation with PC1 but with PC3, -0.66 , $P < 0.05$) and percentage agriculture in the wetland complex (now also with PC3, $+0.64$, $P < 0.05$).

Biodiversity, expressed as the number of red list angiosperms or birds, varied substantially among wetland complexes (Table 4), but these numbers did not differ significantly among the three types of wetland distinguished (Table 4). The maximum number of red list plant species observed in a km^2 -grid square was 39, whereas for birds this was 22 (Table 4). Means, medians, maxima and standard deviations of these indicators across wetland complexes all co-varied significantly (r^2 over 0.54, P always < 0.05), i.e. when the mean number was high in a particular complex, also the maximum and the variability expressed as standard deviation were high. Thus, within these wetland complexes, only limited areas had high numbers of rare and protected species. Plant nor bird biodiversity indicators were correlated significantly

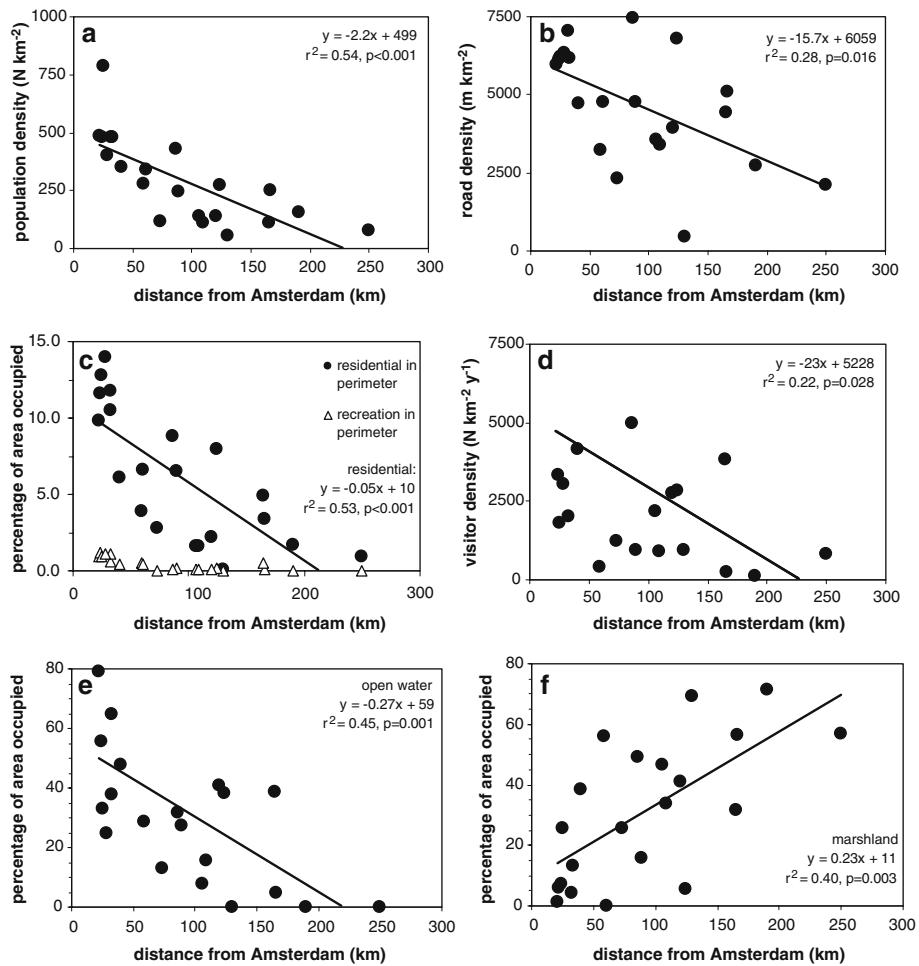


Fig. 2 (a) Human population density, (b) road density, (c) percentage of perimeter occupied by residential and recreational housing, (d) visitor density, (e) percentage open water, and (f) percentage marshland for 20 wetland complexes in The Netherlands plotted against distance to Amsterdam, the capital

with distance to Amsterdam (Fig. 3a), or to any other variable reflecting population density or land use intensity in a simple, linear fashion. Also, the number of red list bird species and plants did not co-vary significantly (Fig. 3b). When only the wetland complexes on peat were considered, we found a significant positive correlation of maximum red list plant species with the proportion of marshland in a stepwise multiple regression ($r^2 = 0.50$, $P < 0.01$). Thus, presence of endangered plants increased with the available area of marshland habitat, but this was not apparent for birds.

Discussion

Our primary aim was to establish the degree of variability in two simple indicators of biodiversity and in a range of potentially causal factors among wetland complexes in

Table 3 Correlation of land use variables within and around the 21 wetland complexes with the first three components of a principal component analysis (81 % explained variance)

| Variable | PC1 | PC2 | PC3 |
|----------------------------------------------------|-------|-------|-------|
| <i>Outside wetland complex</i> | | | |
| Distance to Amsterdam | -0.82 | +0.12 | -0.05 |
| Population density | +0.84 | +0.34 | +0.17 |
| Visitor density | +0.65 | +0.11 | -0.71 |
| Road density in perimeter | +0.89 | +0.25 | +0.05 |
| Percentage area residential in perimeter | +0.94 | -0.05 | +0.23 |
| Percentage area recreation in perimeter | +0.85 | -0.08 | +0.25 |
| Fertilizer Nitrogen application | +0.57 | +0.23 | -0.40 |
| <i>Inside wetland complex</i> | | | |
| Percentage marshland in wetland | -0.84 | -0.14 | +0.07 |
| Percentage agriculture in wetland | +0.27 | +0.77 | +0.44 |
| Percentage forest in wetland | +0.33 | -0.64 | +0.48 |
| Percentage residential and recreational in wetland | +0.40 | +0.72 | +0.30 |
| Percentage water in wetland | +0.78 | -0.01 | -0.57 |
| Percentage covered by roads in wetland | -0.03 | +0.92 | -0.01 |

The three components explained 50, 19 and 12%, respectively of the total variability. The first component is interpreted as a complex of factors interrelated to urbanisation and population density, the second to agricultural land use within the wetland complexes and the third to recreation on water. Correlations over 0.43 are significant at $P = 0.05$ and those over 0.55 at $P = 0.01$ (italicized here)

Note, a varimax rotation converged in 6 iterations, but did not alter the pattern and explained variance compared to that after initial extraction. The latter is therefore shown here

The Netherlands. Indeed, present-day patterns in the distribution of rare species across these wetland complexes displayed substantial variation, and for red list plants in peatlands, one particular type of wetland, this was correlated to the availability of open marshland. This variable correlated negatively with the first urbanisation-related principal component. For riverine or coastal wetland complexes, however, we could not detect any co-variability among our biodiversity indicators and those of land use, recreation or fragmentation. Furthermore, bird diversity was not affected markedly by any of the factors quantified here. We conclude that wetland red list birds are probably less sensitive to either form of human interference, as quantified here, than angiosperm plants.

The co-variability among our different indicators of land use suggests that a separation of agriculture and urbanisation as different causal agents is not straightforward. Intensity of fertilizer use by agriculture covaried with the first urbanisation/population density-related PCA-axis, but area occupied by agriculture and road density within the wetland complex did so with the second PCA-axis. Also visitor density illustrates this multicausal variability: it correlated both with the first PCA axis and with the third, which was linked to the area of open water in a wetland. Together, these patterns reveal the existence of a distinct gradient in population density and urbanisation across some 250 km in the Netherlands, with two separate, but less important gradients superimposed.

Our results may prompt several questions, related to the spatial resolution, the appropriateness of the indicators of biodiversity (taxonomic resolution and completeness or congruence), and of those of human impact. We argue here that the applied spatial resolution (km^2 and wetland complex) serves well when aggregate questions of overall, regional variability in species richness is the target, as in

Table 4 Means and ranges of indicators of biodiversity, wetland complex land use and fragmentation and recreation pressure as well as of the surrounding perimeter with a 10 km radius. Means are broken down over the three types (Table 2) and presented with standard error

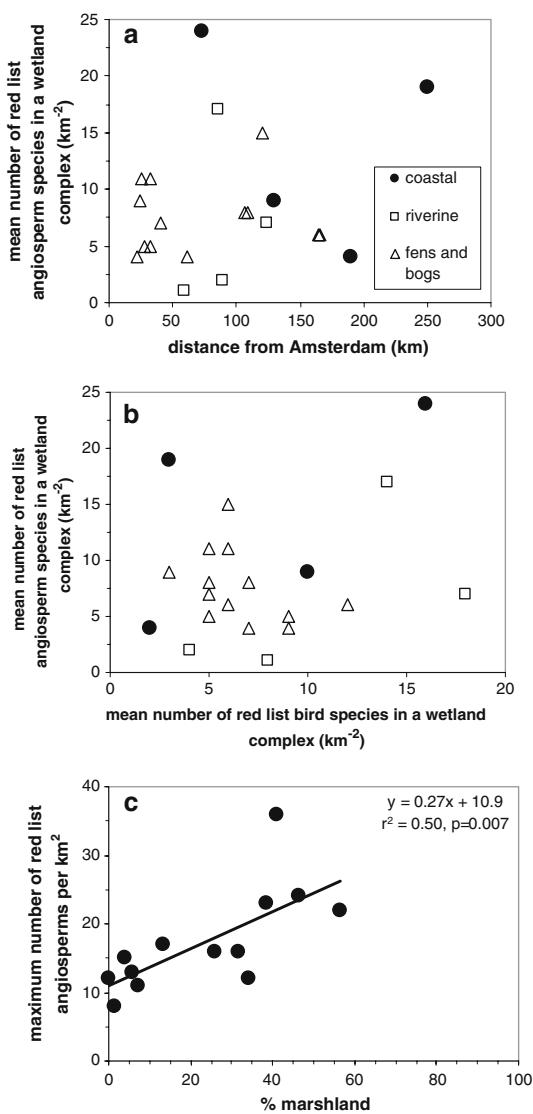
| Variable | Coastal | Riverine | Fen or bog | Total range |
|-----------------------------------------------------------------------------------------------------------|--------------|--------------|--------------|-------------|
| <i>Biodiversity</i> | | | | |
| Mean number of red list angiosperm plant species over all km ² -squares in the wetland complex | 14 ± 5 | 7 ± 4 | 8 ± 1 | 1–24 |
| Maximum number of red list angiosperm species | 24 ± 6 | 11 ± 4 | 17 ± 2 | 3–39 |
| Standard deviation of the number of red list angiosperm species | 5 ± 1 | 3 ± 1 | 4 ± 1 | 1–9 |
| Mean number of red list bird species | 8 ± 3 | 11 ± 3 | 7 ± 1 | 2–18 |
| Maximum number of red list bird species | 12 ± 5 | 16 ± 2 | 11 ± 1 | 4–22 |
| Standard deviation of red list bird species | 2 ± 1 | 4 ± 1 | 3 ± 1 | 1–6 |
| <i>Wetland complex</i> | | | | |
| Percentage of the area covered by marshland (all % km ⁻²) | a 56 ± 11 | ab 32 ± 12 | b 24 ± 5 | 0.2–72 |
| Percentage agriculture | a 1 ± 1 | b 17 ± 4 | ab 16 ± 5 | 0–66 |
| Percentage forested | 3 ± 3 | 9 ± 4 | 15 ± 4 | 0–38 |
| Percentage built-up (residential and recreational) | 0 | 0 | 1.1 ± 0.7 | 0–9 |
| Percentage open water | a 3 ± 3 | ab 32 ± 3 | b 41 ± 7 | 0–88 |
| Percentage covered by roads | 0.7 ± 0.3 | 0.8 ± 0.2 | 0.8 ± 0.2 | 0–2 |
| Visitor density (number km ⁻² y ⁻¹) | 789 ± 240 | 2307 ± 1040 | 4087 ± 936 | 119–11111 |
| <i>Surrounding perimeter</i> | | | | |
| Distance to Amsterdam (km) | 161 ± 38 | 90 ± 13 | 72 ± 15 | 22–250 |
| Population density (number km ⁻²) | 103 ± 23 | 309 ± 42 | 350 ± 55 | 54–786 |
| Percentage of area covered by residential housing | 1 ± 1 | 7 ± 1 | 7.5 ± 1 | 0.1–14 |
| Percentage covered by recreational facilities | 0 | 0.3 ± 0.1 | 0.6 ± 0.1 | 0–1 |
| Density primary roads (m km ⁻²) | a 111 ± 40 | b 323 ± 35 | b 388 ± 32 | 0–539 |
| Density secondary roads (m km ⁻²) | a 1796 ± 463 | b 5231 ± 958 | b 4824 ± 298 | 450–7030 |
| Nitrogen use as fertilizer by agriculture in 2002 (kg ha ⁻¹) | a 96 ± 18 | a 133 ± 27 | b 245 ± 12 | 62–327 |

When these three differ significantly (Tukey test, EER = 0.05, CER = 0.017) this is denoted with lower-case lettering, where means sharing the same letter do not differ. The last column gives the total range observed across the 21 wetland complexes studied

nationwide assessments (Andelman and Fagan 2000; Cornwell and Grubb 2003). The appropriateness of our indicators could have been questioned due to the constraint of data availability. We argue that our indicators are sufficiently appropriate for local conservation practice, since we used red-list taxa. The usefulness of vegetation as a biodiversity indicator has been stressed before (Dobson et al. 1997; Kati et al. 2004).

We have stressed before that our observations reflect present day patterns, which may have causes that are still operational or have been so in the past only. The percentage of open water in a complex, for example, is closely related to the distance to Amsterdam, as a surrogate for the densely populated part of the country. This probably has its roots in the large-scale 16th and 17th century peat excavation

Fig. 3 (a) mean number of red list angiosperm plant species per square kilometer in three different types of wetland complexes plotted against distance to Amsterdam; (b) scatter plot of red list plants against red list birds for the same three types of wetlands; (c) maximum angiosperm red list species density in thirteen fen- and bog wetlands as a function of the proportion of marshland. When absolute area was used instead of percentage in the wetland complex, the r^2 increased to 0.75



activities, and the adjacency of urban markets. However, this major landscape pattern has become fixed in the 20th century when open water came to serve recreation as a new economical strength and succession into reed beds and fenland came to a standstill, whereas existing fens turned into alder or willow carr (Bakker et al. 1994; Van Diggelen et al. 1996). Thus, the temporal dynamics of these wetland landscape complexes were probably greatly reduced (Verhoeven 1992; Graveland 1998). It is difficult to argue decisively how much this has affected biodiversity patterns when many angiosperm taxa are long-lived and dispersal capacity is insufficiently known (Ozinga et al. 2005), but habitat availability must have been reduced greatly, particularly for herbaceous fens and marshes of low nutrient availability (Soons et al. 2005), and this will have reduced the extent of surviving populations of a number of

habitat specialists that feature on red lists. Restoration efforts targeted at these habitats appear justified (Beltman et al. 1996). We conclude that wetland plant biodiversity reduction presently is primarily due to habitat loss coupled to this major complex of regional-scale urbanisation-related factors.

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Translocation of an endangered insect species, the field cricket (*Gryllus campestris* Linnaeus, 1758) in northern Germany

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Abstract Relocations of species have become a tool widely used in nature conservation, but insects have rarely been considered as targets. Here, we present a translocation project of the field cricket (*Gryllus campestris* L. 1758), which is a threatened species at the northern edge of its range. Only ten populations were left in Lower Saxony (Germany), illustrating the need for urgent conservation measures. After 10 years of monitoring and management of an isolated population, 213 nymphs were captured and released at another nature reserve in summer 2001. The size of the new population increased significantly from 27 singing males in spring 2002 to 335 singing males in spring 2005. The occupied area increased from 5.66 ha to 33.14 ha. Altogether, the translocation project was evaluated as successful, but the inland dune proved to be not as suitable for the species as initially expected. Our results indicate that translocations of highly reproductive insect species are promising, as long as the release locality contains sufficiently large areas of suitable habitat and a high number of wild juveniles from a closely located and large source population are released in a climatically favorable period. Management and restoration of habitats, as well as continuous monitoring are of crucial importance for the success of the translocation project. Moreover, the importance of a high quality of cooperation between conservationists, authorities, foresters, farmers, financiers and scientists cannot be overstated.

Keywords Heathland · Insect conservation · Orthoptera · Re-introduction · Relocation · Restoration

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Introduction

Animal relocations have become a widely used tool in conservation management. However, most re-introduction projects so far have focused on large vertebrates, such as birds and mammals (Sarrazin and Barbault 1996; Fischer and Lindenmayer 2000). In spite of the fact that invertebrates constitute a substantial proportion of the species richness and biomass, and play a significant role in ecosystem functioning, they rarely have been considered as relocation targets and are even often discounted in conservation management as a whole. Thus, invertebrates need to receive much more attention in nature conservation (Pyle et al. 1981; Dunn 2005). Relocation projects of highly reproductive invertebrates are much more promising than those of large vertebrates due to their small body size, the low costs, and the small spatial requirements (Pearce-Kelly et al. 1998). The few documented cases of invertebrate relocations mainly deal with Lepidoptera species (Rawson 1961; Dempster et al. 1976; Duffey 1977; Väisanen et al. 1994; Witkowski et al. 1997), but some examples of Orthoptera relocations have also been published (Pearce-Kelly et al. 1998; Sherley 1998; Berggren 2005).

Four different types of relocations are commonly distinguished (IUCN 1998): Re-introductions (attempts to establish a species within its historical range), translocations (attempts to establish new populations within the range), supplementations (addition of individuals of different genotype to an existing population), and conservation introductions (attempts to establish a species outside its natural range, but in an appropriate habitat). The aim of translocation projects is usually to reduce the risk of extinction for an endangered species by creating more self-sustaining populations (Sherley 1998). Fragmentation of habitats and loss of (sub-)populations have been recognized as main threats for many species (Primack 2002). The artificial establishment of new populations is, therefore, a consistent method for enhancing the survival probability of a species. However, only 26% of the relocation trials analyzed in a recent review have been classified as successful (Fischer and Lindenmayer 2000). There is a strong need for more thorough management of relocation experiments, with careful background research, choice of suitable release sites and release stocks, as well as monitoring before and after the relocation (IUCN 1998; Fischer and Lindenmayer 2000). Here we present the results of a translocation experiment of the field cricket (*Gryllus campestris* L. 1758) in northern Germany. We evaluate the success of the translocation project by using a strong criterion (significant increase in population size) as indicator of the success.

Methods

The study object

The field cricket (*Gryllus campestris*) is a rather well-known insect. It is a comparatively large cricket species (17–26 mm), characterized by a shiny black body coloration (Marshall and Haes 1990). The species mainly inhabits dry grasslands, and is restricted to heathlands and oligotrophic grasslands at the northern edge of its range (Kleukers et al. 1997), where it typically lives in burrows of approximately 30 cm depth (Regen 1906). The reproductive season of the univoltine species lasts from May until the end of June. Nymphs hatch in mid July and overwinter during

their tenth or eleventh instar (Köhler and Reinhardt 1992). The final moult takes place at the end of April or at the beginning of May. While males are territorial and defend their burrows fiercely, females are vagrant and are attracted by singing males. They lay their eggs in bare ground either close to a burrow or into the burrow. The first instars can be found under bark or wooden pieces, but they also use old burrows of adults. Populations of *G. campestris* are known to undergo extreme fluctuations and are strongly affected by weather conditions (Remmert 1992).

The field cricket is a threatened species at the northern edge of its range, such as the UK (Pearce-Kelly et al. 1998), Germany (Ingrisch and Köhler 1997), the Netherlands (Kleukers et al. 1997), Denmark (<http://redlist.dmu.dk>, 2006) or Switzerland (Thorens and Nadig 1997). In Lower Saxony it is listed as Critically Endangered (Grein 2005), with only ten populations left (Grein 2000). The main reason for its decline is believed to be habitat loss. Due to its well-known song, the field cricket is a comparatively popular insect species. It probably represents one of the scarce examples of “non-butterfly insects”, which are suitable as flagship species. For this reason, the species has been selected as *Insect of the Year 2003* by the “Kuratorium Insekt des Jahres” of the German Entomological Institute (Eberswalde) and the Federal Biological Research Center for Agriculture and Forestry (Braunschweig) in Germany. In Lower Saxony, only one isolated population remained west of the river Weser, at the eastern edge of the nature reserve “Neustädter Moor”. This population has been monitored and managed intensely during the last 15 years by the non-governmental organization BUND (“Bund für Umwelt und Naturschutz Deutschland” or “Friends of the Earth - Germany”). From 1991 to 2001, the population increased from 32 to 949 singing males (Hochkirch 1996; Teerling and Hochkirch 2002). In order to reduce the extinction risk further, a translocation project was started in 2001, intending to establish a second self-sustaining population in a nearby nature reserve (“Renzeler Moor”). Although there are no former records of field crickets available for this nature reserve, it consists of many seemingly ideal but unoccupied habitats for field crickets and was thought to enable them to spread further. However, it is separated from the source population by a distance of 3.5 km, with the river “Große Aue” and wet grasslands acting as effective barriers for these flightless insects.

The study area

The two study sites are located in the central part of the natural region “Diepholzer Moorniederung”, an area between the towns Hannover, Bremen and Osnabrück (Lower Saxony, Germany). The region is characterized by large peat bogs, wetlands and dry alluvial sand ridges. These dry areas are naturally oligotrophic and were heavily overgrazed from the middle ages to the 19th century. During this period, heathlands, dunes and oligotrophic grasslands spread over northern Germany (Webb 1998). After the invention of artificial fertilizers and massive changes in land use, only small fragments of heathland have been left (Bakker and Berendse 1999). All peat bogs are strongly degraded, either by cultivation, peat cutting or dehydration. At the beginning of the 1970s, regional conservationists started a conservation project in order to save the remaining peat bog fauna, which has been continued by the BUND since 1983. With increasing experience the field of activities spread to other types of habitat, such as wet grasslands, dunes and heathlands, which surround the peat bog areas.

The nature reserves in the “Neustädter Moor” include the peat bog, as well as adjacent heathlands and wet grasslands at the western edge. The main part of the source population occurs east of these reserves, but it has spread into them during the last decade (Teerling and Hochkirch 2002). We chose two release sites on a former inland dune system in the northwestern part of the nature reserve “Renzeler Moor” (established in 1970). This area was used as farmland and pine forest during the past decades and transformed into meso- to oligotrophic grasslands at the beginning of the 1990s. Both reserves are maintained by extensive sheep grazing, which is also known to be advantageous for field crickets (Schmidt 1998).

The translocation procedure

From 1990 to 2001, the population at the Neustädter Moor was intensely monitored and managed, leading to an approximately 30-fold increase in population size. In 2001 the population size was sufficiently large to start the translocation procedure, which was oriented towards a previous re-introduction project for the field cricket in England (Pearce-Kelly et al. 1998). The release sites at the Renzeler Moor were inspected by the authors and an additional expert (G. Grein) and there was general agreement that they represent suitable habitats for the field cricket. However, a detailed habitat analysis was not performed. Two localities were chosen as release sites: a meso- to oligotrophic pasture, which was managed by sheep grazing since 1992 and a restored inland dune, which was formerly forested with pines and deforested in the winter of 1990/91. The great habitat-diversity of the surrounding terrain was expected to allow further dispersal to suitable sites during the following years. Since the success of translocations can be increased by using wild animals as a source, releasing a large number of individuals and removing any detrimental factors (Fischer and Lindenmayer 2000), we followed these recommendations. In contrast to the breeding program presented by Pearce-Kelly et al. (1998), only wild nymphs were released during the translocation. Although the source population could be genetically rather invariable due to a bottleneck in 1991 (32 singing males), it was chosen to gain nymphs only from this well-monitored area, which is also the closest population to the release area. In order to increase the genetic diversity as far as possible, nymphs were collected from different subpopulations at the Neustädter Moor. The populations of both release and source area were monitored during the following years.

A total of 213 nymphs (instar 7–8) were collected on 4 days in July 2001. They were stored in boxes with swards of grass and heather to enable the nymphs to find shelter beneath them during the transportation. Fish food was supplied until they were released on 31 July 2001. Approximately half of the individuals (113 specimens) were introduced directly on the inland dune, the other half (100 specimens) on the pasture. Individuals from all subpopulations were released at each site to increase the genetic variability. During the first days pieces of bark were placed on the ground as shelter.

Monitoring of the field crickets

The population size of *G. campestris* in the Neustädter Moor and Renzeler Moor was estimated by counting the number of singing males on each occupied site. The characteristic calling song of the field cricket is well suited for monitoring, since it

can be heard up to 100 m, allowing a fast and comprehensive survey (Detzel 1998). Females and non-singing males were ignored, to allow comparability of the data between different years. Since not all males sing simultaneously, the data have to be regarded as minimum values. The study sites were checked on dry, warm and windless days during the main calling phase (from May to June). Densely populated sites were mapped preferably during the highest activity in the late afternoon or in the evening. All records were transferred to a map and analyzed with ArcView GIS 3.2. This method has been applied since 1990 in the study area (Hochkirch 1996; Teerling and Hochkirch 2002).

Statistical analysis

We computed a linear regression model for population growth for the whole population as well as for three different habitat types (pasture, dune, peat bog) and tested for a positive increase in population size. All data were log-transformed prior to statistical treatment to comply with the model assumptions. The tests were carried out in “R 2.1.1” (R Development Core Team, 2004).

Results

In total, 27 singing males were recorded in the Renzeler Moor in the spring of 2002 (Fig. 1). Assuming a balanced sex ratio, this corresponds to a survival rate of 25.4%. Considering that *G. campestris* is known to have a high mortality during the winter (Remmert 1992), the survival rate was surprisingly high. This led to the decision, not to supplement cricket nymphs in 2002. In the following year, 42 stridulating males were counted and the population had spread also spatially compared with 2002 (Fig. 1). Most of the males were found between the dune and a degraded part or the bog. After the unusual hot summer of 2003 (Ciais et al. 2005) the population increased up to 107 stridulating males in spring 2004. The majority of individuals (70%) were recorded on the pasture, whereas only 7% inhabited the inland dune (Fig. 2). In 2005, the population had grown immensely, reaching 335 stridulating males. Again the majority of crickets (77%) inhabited pastures and bog sites surrounding the inland dune (Fig. 2). Some initial subpopulations colonized sites approximately 250 m outside the nature reserve, such as adjacent fields and meadows. The occupied area increased from 5.66 ha in 2002 to 33.14 ha in 2005 (Fig. 1).

The overall population growth was significantly positive (linear regression model, $df = 2, t = 7.55, p = 0.017, R^2 = 0.9661$) and so was the increase of the occupied area (linear regression model, $df = 2, t = 4.53, p = 0.046, R^2 = 0.911$). However, after analyzing the data for the three habitats (dune, bog, pasture) separately, the subpopulation growth on the dune was not significant (linear regression model, $df = 2, t = 0.910, p = 0.459, R^2 = 0.293$), while the subpopulations increased significantly on the pasture (linear regression model, $df = 2, t = 8.695, p = 0.013, R^2 = 0.974$) and in the bog (linear regression model, $df = 2, t = 10.39, p = 0.009, R^2 = 0.982$).

Discussion

Four years after the translocation of cricket nymphs, we evaluated the project as successful. The population persisted and increased significantly, indicating a high

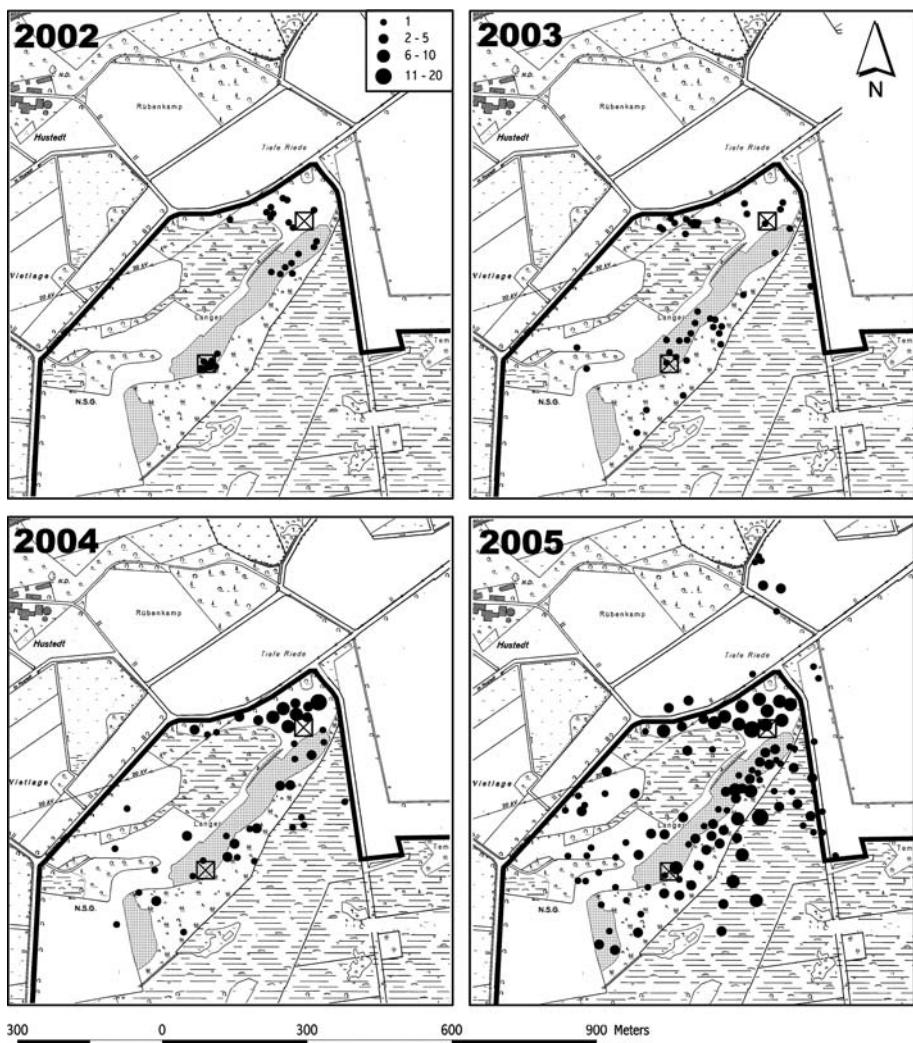


Fig. 1 Dynamics of the new population of *Gryllus campestris* in the Renzeler Moor from 2002 to 2005 (black dots: singing males). The crossed squares represent the two release localities, the southern of which was located on the inland dune, the northern on a pasture. Peat bog sites (striped) are mainly situated southeast of the inland dune. The bold line marks the border of the reserve. Sites north of the reserve consist mainly of conventional farmland

quality of the release area as habitat for *Gryllus campestris*. However, despite of these overall results, the suitability of single sites (or habitat types) differed from our expectations. While the population size increased strongly on the pasture and degraded peat bog, the inland dune turned out to be much less suited than expected (Fig. 2). A possible reason for this might be found in inappropriate conditions for digging burrows (Köhler and Reinhardt 1992), due to either the dense cover of mosses and plant litter or the soil structure of the dune. As initially intended, the increase in population size also caused a considerable dispersal of the field cricket into adjacent areas. Some of these habitats, such as peat bog sites or arable fields, might not be

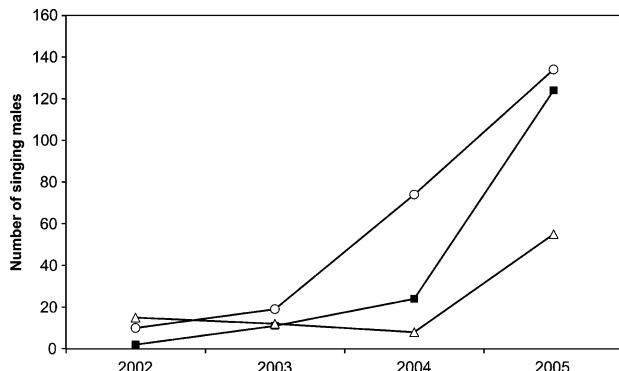


Fig. 2 Comparison of the population development between the three main habitat types: grassland (open circle), peat bog (closed square), dune (open triangle)

suitable as persistent habitats, but they may serve as stepping stones for future expansion. In the source area (Neustädter Moor), degraded peat bog has been colonized permanently during the last decade, allowing dispersal to remote heathlands. Continuous monitoring of the source population showed that the loss of 213 nymphs had no negative consequences. In 2005, the source population reached a new maximum of 1945 singing males (unpublished data). We consider ten factors as crucial for the success of the translocation method, which can be grouped into three major classes: ecological factors, translocation procedure, scientific and administrative support.

Ecological factors

Four ecological factors were probably of importance for the success. (1) The habitat quality in the release area was rather high, due to an intense habitat restoration and management since the end of the 1980s. Continuous management by sheep grazing and mowing is needed to counteract the increased nitrogen deposition from the atmosphere (Bakker and Berendse 1999). Although the dune was less suited for *G. campestris*, deforestation and extensive sheep grazing supported the development of large suitable habitats. The availability of high quality habitat is known to be the major determinant for the success of relocation projects (Rawson 1961; Griffith et al. 1989; Wolf et al. 1996; Sarrazin and Legendre 2000). (2) The high habitat heterogeneity (grasslands, degraded peat bog, dune) in the release area supported the success, as the field crickets were able to choose optimal sites and microhabitats. Orthoptera are known to perform an active habitat choice (Whitman 1987). Moreover, even less suited sites could be colonized in optimal years and serve as stepping stones for future dispersal (Hochkirch 1996). (3) The weather conditions were suitable for population growth from 2003 to 2005. This is probably of crucial importance, since field crickets (as many insects) are highly dependent on favorable weather at the northern edge of their range, which can influence the success of translocation projects immensely (Pearce-Kelly et al. 1998). From 2002 to 2003, the weather conditions were unfavorable (rainy), which is illustrated by a lower population growth (Fig. 2). Apparently, the habitat quality of the pasture was even

suitable under these conditions, since the population persisted and increased slightly in that year. (4) *Gryllus campestris* is a univoltine species, which is known to produce high egg numbers leading to rapid population growth (Remmert 1992; Pearce-Kelly et al. 1998). Demography is generally thought to be of high importance for population survival (Lande 1988).

Translocation procedure

We distinguish four major parameters of the translocation procedure, which assured the success. (1) Differently to the project of Pearce-Kelly et al. (1998) we had the chance to gain specimens from a sufficiently large wild population. Relocation projects using wild animals are generally more successful than those using captive animals (Griffith et al. 1989; Fischer and Lindenmayer 2000). Moreover, translocation success of wild-caught animals correlates positively with the density and increase of the source population (Griffith et al. 1989), which was also true for the population at the Neustädter Moor. (2) As the source population was located close to the release area, the translocated individuals were probably genetically adjusted to the local conditions. The higher success of translocations using founder groups from indigenous sources has been reported also from other taxa (Ebenhard 1995; Sarrazin and Barbault 1996; Singer et al. 2000). (3) Another important factor could be the use of nymphs for the translocation. Nymphs of *Gryllus campestris* are more mobile than adults, since they do not show any territoriality. They do not start to dig burrows before autumn (Detzel 1998). Results from population modeling suggest that the use of juveniles in translocation projects is generally more efficient than relocating adults (Robert et al. 2003). (4) We transferred a high number of individuals. It is noteworthy to mention that the relation between translocation success and the number of animals released is asymptotic (Griffith et al. 1989). Pearce-Kelly et al. (1998) introduced between 106 and 1200 nymphs of *G. campestris*, but the survival depended more upon the habitat quality than on the number of released insects. Although there is a minimum number of animals that should be released, translocations have low chances of success without high habitat quality (Griffith et al. 1989; Ebenhard 1995).

Scientific and administrative factors

Two factors within this class were of importance for the translocation project. (1) Continuous monitoring of both source and release population has been performed since 1990, allowing the assessment of the translocation method as well as the influence of the removal of specimens from the source population. In many translocation projects, such intense monitoring measures are missing (Sarrazin and Barbault 1996). Moreover, the experience of ten years of monitoring and management facilitated the choice of suitable release sites. (2) The success of the translocation project was also promoted by the excellent cooperation of the local and regional administrations, foresters and farmers, financial supporters (see acknowledgements), the executing organization (BUND) and the scientific consultants (University of Osnabrück). There is a strong need for such a high quality of cooperation in nature conservation (Sarrazin and Barbault 1996).

Negative factors

Two factors could have had negative effects on the success of the translocation process. (1) The transferred crickets were gained from only one population, which passed through a genetic bottleneck at the beginning of the 1990s. It is rather likely that the established population is genetically impoverished as has been shown for other translocated populations (Stockwell et al. 1996). However, inbreeding need not always cause inbreeding depression (Lande 1988; Hoelzel et al. 1993; Leberg 1993) and the consequences of genetics on survival or reproduction are difficult to predict (Sarrazin and Legendre 2000). The strong population growth of the field cricket indicates that currently the suggested loss of genetic diversity does not cause any problems. Demography generally seems to be of higher importance for population dynamics than population genetics (Lande 1988). Moreover, by transferring specimens from a nearby locality, the risk of outbreeding depression is minimized (Griffiths et al. 1996, Sarrazin and Barbault 1996). (2) There is another caveat, which should receive a stronger consideration in future translocation projects. Based upon the initial inspection of the release area, two sites (the dune and the pasture) were regarded as suitable habitats for the field cricket. While the subpopulation on the pasture increased continuously from 2002 to 2005, the subpopulation on the dune decreased during the first three years (Fig. 2). The increase of the dune subpopulation in 2005 might be caused by continuous immigration from the surrounding sites. The success of the whole project was determined by the high performance of the pasture and the surrounding bog sites. Had only the dune been chosen as a release site, the project might have been less successful. Therefore, detailed habitat analyses should be performed prior to relocation projects (Holloway et al. 2003).

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Conservation of taxonomic and biological trait diversity of European stream macroinvertebrate communities: a case for a collective public database

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Abstract The use of databases for the conservation of biodiversity is increasing. During the last decade, such a database has been created for European stream macroinvertebrates. Today, it includes 527 sites that are the least human-impacted representatives of many stream types across many European regions. It includes data on the abundance of 312 invertebrate genera, several environmental site characteristics, collection methods, bibliographic data sources, and 11 biological traits of the genera (e.g. size, life cycle, food and feeding habits, described in 61 categories). The database will be useful in addressing many topics that are potentially relevant to biodiversity conservation. To illustrate this potential, we provide examples of how the data could be exploited. First, we describe the frequency of some taxonomic and biological characteristics (e.g. richness and diversity of genera and traits) of the macroinvertebrate communities and assess how these characteristics are related (e.g. how trait richness increases with genus richness). Second, we describe the frequency of some characteristics of the genera and traits (e.g. occurrence frequency, abundance, dispersion index) and again assess how these characteristics are related (e.g. how occurrence increases with abundance). Finally, we suggest how the database could be developed into a collective, publicly accessible database that covers stream types and regions of Europe more comprehensively.

Keywords Abundance · Contagious distribution · Dissimilarity · Occurrence frequency · Rarity · Relationships · Richness · Trait categories

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Introduction

Databases are increasingly used for biodiversity conservation (e.g. Freitag et al. 1997; Roberts et al. 2005). Traditionally, such databases appeared in printed format for ecosystems of a given region (Seely et al. 2003) or for particular taxonomic groups (Van Swaay and Warren 1999) and the data of the latter were subsequently used to address particular conservation issues, for instance identification of biodiversity hotspots (Werner and Buszko 2005). Others assembled printed information in digital formats to study particular questions of biodiversity conservation, but this digitized information was not accessible to the public (e.g. Lei et al. 2003). In contrast, several digital databases that will facilitate the conservation of biodiversity are planned or are being implemented, including those of Gachet et al. (2005) and Roberts et al. (2005), and see the following websites: <http://www.sciencemag.org/feature/data/biodiversity2000.dtl#global>; <http://www.worldwildlife.org/wildfinder/>; <http://www.guadalmed.org>; <http://www.faunaeur.org/>; <http://www.freshwaterlife.org/>; <http://www.leda-traitbase.org/>. Although there has been debate about what information such publicly accessible databases should provide (see Smith et al. 2000), we obviously need more of them for rapid transfer of scientific knowledge to those who make biodiversity conservation decisions.

Typically, the creation of public databases transferring knowledge for conservation requires well-organized networks and substantial funding (Roberts et al. 2005; <http://www.gbif.org/>). Alternatively, one could provide public access to a database that has been used previously to address specific research questions, and it is this alternative we opted for, hoping that others will add their own data to this database. Our data are on benthic stream macroinvertebrates that were studied at 527 sites that included the least human-impacted representatives of many regional stream types across many parts of Europe. The data include the abundance of 312 genera, several site characteristics, details of collection methods, and bibliographic data sources. The data were assembled and used by Charvet et al. (2000) and Statzner et al. (2001a, 2004), and with the addition of a substantial amount of Mediterranean data, will be used by us in comparisons of diversity patterns between temperate and Mediterranean climates. These data enable traditional, taxonomic diversity assessments for a group of organisms that has so far not been the focus of freshwater conservation, which has been on a few better known groups such as fish, crayfish and molluscs (Lévéque et al. 2005) that may have different diversity patterns from those of insect-dominated invertebrate communities (Heino et al. 2005).

In addition, the database contains data on 11 biological traits (e.g. size, life cycle, food and feeding habits, described in 61 categories) that provide more general information on the biological diversity of communities and facilitate the interpretation of taxonomic biodiversity patterns, including losses (e.g. Jennings et al. 1999; Gachet et al. 2005). These trait data were assembled and used by multiple authors in the volume edited by Statzner et al. (1994) and in subsequent studies by Dolédec et al. (1999), Usseglio-Polatera et al. (2000), and Tachet et al. (2002); we have since added information on some Mediterranean genera to the database.

Because of the lack of consistent, species-level information, the database is limited to genera, which is regrettable for taxonomic biodiversity assessments. For assessment of biological trait diversity, however, this is less of a problem, as using genera instead of species scarcely affected the description of the trait composition of stream invertebrate communities (Dolédec et al. 2000).

The general structure of our database will enable the assessment of many topics that are potentially relevant for conservation, including the following. What is the frequency of the genus/trait richness in almost natural communities of a given European region/stream type? Is this richness related to the overall invertebrate abundance in these communities? What is the regional frequency of the overall invertebrate abundance in a given stream type? Is the biological trait diversity of invertebrate communities related to their taxonomic diversity? Is the taxonomic/trait composition of a given community rare in comparison to other communities? Is the occurrence of traits in communities influenced by phylogenetic constraints? How different is the taxonomic/trait composition between communities from temperate and Mediterranean climates? Which genera/traits are rare and which not? Is this rarity limited to some regions/stream types? Is the rarity of genera associated with particular biological traits? Which genera/traits frequently or rarely co-exist in the communities of a region/stream type? And, addressing the need for improved identification tools, which genera occur frequently and/or in high abundances so that reliable species-level identifications are very often required in traditional taxonomic biodiversity assessments? This list of questions is far from exhaustive, and obviously we cannot address all of them here.

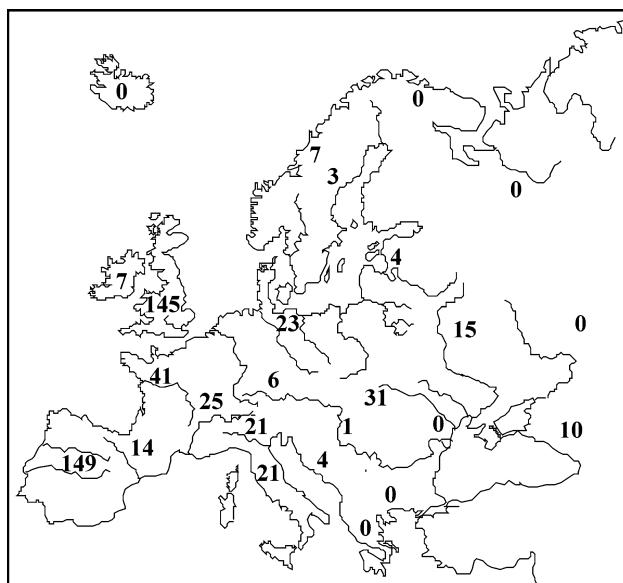
In this paper, we briefly describe the data and then give a few examples of how the database could serve conservation. We select examples corresponding to our objective to outline a large framework for potential research and applications, rather than detailed assessment of a particular topic. First, we describe the frequency of some taxonomic and biological characteristics (e.g. richness and diversity of genera and traits) of the macroinvertebrate communities (in overall terms) and assess how these characteristics are related (e.g. how trait richness increases with genus richness). Second, we describe the frequency of some characteristics of the genera and traits (e.g. occurrence frequency, abundance, dispersion index) and again assess how these characteristics are related (e.g. how occurrence increases with abundance). Finally, we suggest how our database could be developed towards a collective, publicly accessible database that covers stream types and regions of Europe more comprehensively.

Description of the database and methods

Invertebrate abundance data, collection methods, and environmental site characteristics

The invertebrate abundance data (individuals m^{-2}) included in the database were from sites that were among the least human-impacted representatives of regional stream types according to the following criteria: (1) rating by authors of the data (either in the data source or as personal communication); (2) biotic indices indicated good environmental health; (3) site used as reference in comparisons to human-impacted sites; (4) location in a national park or nature reserve; and/or (5) low human impact indicated by site descriptions. From longer time series of invertebrate abundance data, we selected a period that represented one annual cycle. From spatially replicated non-random samples at a site, we generated values as close as possible to the mean abundances of the genera at a site (e.g. by weighting microhabitat samples using the spatial extent of the microhabitat in the stream reach). In

Fig. 1 Locations of the 527 least human-impacted European running water sites currently included in our database in the 25 biogeographical regions defined by the Limnofauna Europea (Illies 1978), with the number of sites in each region plotted at its approximate centre



addition, taxon identifications had to be at or above the genus level, as our trait data considered genera. Given that Oligochaeta and most Diptera were typically not identified to the genus or species level, we excluded them from the data. Despite this omission, abundance data were available for 312 genera (257 of these were insects). For some sites we had to assign the abundance of unidentified taxa (typically less abundant insect families or orders) from other studies of these taxa from similar sites of a given area, i.e. we used the relative abundance of genera in these taxa observed elsewhere in a given area. Given that many of the data sources were relatively old, we used the nomenclature of Illies (1978) and ignored recent taxonomic revisions splitting a former genus into distinct genera (e.g. *Ephemerella* into *Ephemerella* and *Seratella*).

Previous studies provided a database of invertebrate abundances at 384 sites, most from areas with temperate climate (Charvet et al. 2000; Statzner et al. 2001a, 2004). To increase the data for Mediterranean climates, we added abundances at 143 Iberian and French sites from Alba-Tercedor and Jiménez-Millán (1985), Gallardo and Toja (1989), Alba-Tercedor et al. (1990), Ortega et al. (1991), Zamora-Muñoz (1991), Zamora-Muñoz and Alba-Tercedor (1992), Gallardo-Mayenco (1993), Miñano (1994), Moreno (1994, 2003), Picazo-Muñoz (1995), Zamora-Muñoz et al. (1996), Rieradevall and Prat (1997), Martínez et al. (1998), Cazaubon and Giudicelli (1999), Bonada et al. (2000), Guerrero (2002), Acuña (2004), C. Solà (personal communication 2004), C.N. Coimbra and M.A.S. Graça (personal communication 2005), A. Gallardo-Mayenco (personal communication 2005), and M. Vila-Escalé (personal communication 2005). As a result, the data currently represent 527 European sites that cover Europe in a rather uneven way, as most data were available for mainland Britain and the Iberian Peninsula (Fig. 1).

Study methods (e.g. sampling technique, mesh-size use) and seasonal coverage have major impacts on abundance estimates (e.g. Pearson et al. 1973; Barber and Kevern 1974), so we classified and described the methods used at all sites in the

Table 1 Methods used to sample invertebrate abundance data at the 527 sites. These were treated as ordinal variables in the analysis assessing the variation in taxonomic abundance that resulted from use of different methods

| No. of seasons included | Sampling technique | Mesh size (mm) | | | | |
|-------------------------|---------------------|----------------|----------|--------|----|---------|
| | | ≤0.3 | >0.3–0.5 | >0.5–1 | >1 | Unknown |
| One | Surber ^a | 20 | 7 | 1 | 0 | 0 |
| | Kick ^b | 20 | 4 | 0 | 11 | 0 |
| | Others ^c | 0 | 13 | 0 | 0 | 6 |
| Two | Unknown | 0 | 0 | 0 | 0 | 3 |
| | Surber | 15 | 53 | 6 | 0 | 0 |
| | Kick | 53 | 61 | 1 | 0 | 0 |
| Three | Others | 1 | 7 | 1 | 0 | 12 |
| | Surber | 6 | 3 | 2 | 0 | 6 |
| | Kick | 0 | 10 | 15 | 0 | 0 |
| Four | Others | 2 | 12 | 2 | 0 | 7 |
| | Surber | 44 | 34 | 0 | 0 | 2 |
| | Kick | 7 | 51 | 2 | 6 | 0 |
| | Others | 5 | 12 | 1 | 0 | 3 |

^a Includes box, grab, and similar samplers (see Merritt et al. 1978)

^b Converted to individuals m⁻² by approximate estimates using Hynes (1961) and others (see Statzner et al. 2001a)

^c Includes quantitative sampling with nets or scrapers, or of stone surfaces

database. Not surprisingly, since the data were collected over almost a century, the methods used varied and often such basic information as mesh size was not available (Table 1). To evaluate the variability in the abundance data resulting from the use of different methods, we used partial Canonical Correspondence Analysis (CCA) (Ter Braak 1988) on the 488 sites with complete information on methods (see Table 1). For the untransformed abundances of the genera, partial CCA showed that 4.5% of the overall variability was a result of different sampling techniques, mesh-size use, and seasonal coverage. This low influence of methods on the untransformed invertebrate abundance structure (in comparison to the ~20% reported for 346 sites by Statzner et al. 2004) was a result of the inclusion of many Iberian sites, which were sampled with relatively uniform methods (typically kick sampling and very small [≤ 0.3 mm] or small [$>0.3\text{--}0.5$ mm] mesh-size) but varied considerably in the abundance structure of their communities.

The sites could be grouped broadly by altitude, water hardness, and stream width. Categorizing the sites in this way (Table 2) indicated, in a coarse way, water temperature, flow and bottom substrate conditions, oxygen and ion concentration, riparian factors such as shading and leaf litter input, and disturbances caused by temporal flow variation (floods and droughts) at the sites; for example, small, softwater mountain streams have lower water temperature and ion concentration but higher current velocity (and thus coarser bottom substrate), oxygen concentration, leaf litter input (if below the tree line) and flow variation than large, hardwater lowland streams (Gordon et al. 1992; Allan 1995). These characteristics are known to affect the taxonomic structure of stream invertebrate communities; for example, softwater streams often lack molluscs, crustaceans, and leeches (Ward 1992; Allan 1995). In addition, these factors may have effects on the biological trait composition of stream invertebrate communities (e.g. Townsend and Hildrew 1994; Lamouroux et al. 2004).

Table 2 Environmental characteristics of the 527 sites (see text for other environmental characteristics included in the database)

| Altitude (m) | Hardness ^a | Stream size (width, m) | | | |
|----------------------|-----------------------|------------------------|----------------------|-------------|---------|
| | | Small (<10) | Intermediate (10–40) | Large (>40) | Unknown |
| Lowland (<150) | Soft | 31 | 9 | 7 | 0 |
| | Intermediate | 18 | 6 | 1 | 0 |
| | Hard | 53 | 6 | 7 | 4 |
| | Unknown | 1 | 0 | 0 | 1 |
| Highland (150–1,000) | Soft | 79 | 22 | 4 | 0 |
| | Intermediate | 41 | 8 | 0 | 0 |
| | Hard | 112 | 10 | 0 | 1 |
| | Unknown | 8 | 1 | 0 | 3 |
| Mountains (>1,000) | Soft | 47 | 6 | 1 | 0 |
| | Intermediate | 7 | 2 | 0 | 1 |
| | Hard | 12 | 1 | 0 | 0 |
| | Unknown | 0 | 0 | 0 | 17 |

^a Water hardness estimated from a variety of parameters (e.g. national hardness degrees, calcium content, conductivity and/or simply rock/soil descriptions, converting the latter to hardness using Braukmann 1984); typical conductivity ($\mu\text{S cm}^{-1}$) of the categories corresponds to < \sim 200 (Soft), \sim 200 to \sim 400 (Intermediate), and $>\sim$ 400 (Hard)

Statzner et al. (2004) examined such effects on trait composition, so we did not repeat these analyses with the present expanded dataset. However, when describing invertebrate community characteristics, we included short descriptions of the typical environmental conditions associated with extreme (e.g. genus-poor versus genus-rich) communities. For this purpose, we had to address the uneven distribution of sites across geographic regions or stream types (e.g. small versus large streams) by comparing the frequency of environmental conditions associated with extreme communities with the frequency of similar environmental conditions in the entire data.

The short description of the environmental information included in the database illustrates a multitude of options for research on and applications in biodiversity conservation. Altitude was available for all sites and water hardness and stream width was available for most sites, although the number of sites in each category within altitude, hardness, and width varies (Table 2). Overall, sites with soft water predominate above 1,000 m, and there are fewer sites as stream width increases. The database contains only 20 large river sites (>40 m wide) because few of them remained in a natural enough state by the time quantitative invertebrate studies began to be undertaken. In addition to the environmental information in Table 2, the database includes: (1) climate type (temperate or Mediterranean); (2) country name when the data were collected; (3) latitudinal/longitudinal coordinates of the sites; (4) biogeographical region, following Illies (1978); (5) flow (permanent or temporary), that is further detailed for specific stream types such as permanent lake outlets or temporary frozen, dry or intermittent (not flowing but water remaining in pools) sites. Overall, this environmental information can be used to assess biodiversity patterns at finer spatial scales than undertaken herein (focussing on all sites), as well as for particular stream types or across climatic gradients.

Biological trait data

To describe the trait composition of the invertebrate communities we used available information on 11 biological traits described in 61 categories (Usseglio-Polatera et al. 2000; Tachet et al. 2002) (Appendix 1). The selection of these traits and their categorization was dictated by the available information. Some traits directly reflect ecological functions (e.g. food and feeding habits), whereas others are indirect indicators. For example, size indicates also the ratio of production/biomass and of production/respiration, because in lotic invertebrate populations both ratios are closely related to the maximum size achieved by the different taxa (Statzner 1987). Size also has implications for many other ecological functions (Peters 1983).

Using recent nomenclature, Tachet et al. (2002) summarized available knowledge on biological traits accumulated over the 20th century for all easily identifiable freshwater invertebrate taxa of France (typically genera, rarely subgenera). Given that we had to ignore recent taxonomic revisions splitting former genera (e.g. *Ephemera*, see above), we re-organized the trait data for these older genera using the species richness in the recent genera to weight the traits described by Tachet et al. (2002). Likewise, we obtained trait profiles at the genus level (e.g. for *Rhyacophila*) for which Tachet et al. (2002) provided trait information at the subgenus level. With the expansion of the data to include the Iberian area, we had to deal with 17 genera not covered by Tachet et al. (2002). For these genera, we coded the traits as completely as possible in the same way as Tachet et al. (2002) did by assigning an affinity score for each genus to each trait category using a fuzzy coding approach (Chevenet et al. 1994). For example, the maximum size achieved by the species of a genus was divided into seven length categories (Appendix 1). If all European size records for a genus fell into one category, it scored the affinity “3” for that category and “0” for all others. If most European size records fell into one length category but a few lay in a neighbouring category, the genus would score “2” and “1” for the two categories, respectively. If we could not find information on a given trait for a given genus, we coded all its categories “0”. Thus, the trait database describes the overall European affinity of each genus to each trait category. For our database, these category affinities were rescaled so that their sum for a given trait typically equalled “1” (exceptionally “0” if information was unavailable).

Data analysis

Our data analyses addressed the objective of outlining a large framework for the potential assessment of taxonomic and biological trait diversity using our database. Thus, we provide examples of descriptions and relations that could be useful in biodiversity conservation.

To obtain the abundance or proportion of trait categories in a community required linking the traits with the taxonomic community structure (e.g. weighting the traits using taxon abundance or biomass). Therefore, we weighted the rescaled affinity scores of the genera for the 61 trait categories by multiplying the scores of each genus by its abundance, and summed these values by trait category. Thus, the overall trait category abundance at a site was typically 11 times greater than the abundance of all genera (when information on the 11 traits was available for all genera at the site), so we did not include the overall trait category abundance in subsequent site descriptions. To obtain the proportion of categories per trait and site, the

summed (across genera) trait category values were rescaled to add up to 1 for each trait and each site.

For the taxonomic (genera) and biological (trait) composition of the communities, we calculated three indices that have implications for biodiversity conservation. First, the Simpson diversity index (D) as $D = 1 - \sum (p_i)^2$ (separately calculated for the categories of each trait and then averaged across the 11 traits). This commonly used index describes the probability that two randomly chosen individuals belong to different genera (or trait categories). Second, the Bray–Curtis (or Sørensen) dissimilarity of the mean relative abundance of genera and trait categories at each site from the values averaged over all sites, which provides information on the difference of the community composition at a given site from the average community composition. This technique is well-known for taxonomic assessments but for assessments of traits, we calculated half of the sum of the absolute difference between observed (p_{ij}) and mean value at all sites (p_{all}) for all categories (i) of a trait, which provided the dissimilarity per trait for the j sites (i.e. $0.5 \sum |p_{ij} - p_{i\text{all}}|$). Averaged over all traits, we obtained the dissimilarity of a site from the overall mean trait profile at all sites. Third, for each genus and each trait category, we calculated its dispersion index across the sites as abundance variance divided by abundance mean. A dispersion index of 1 indicates random distribution, whereas higher values indicate contagious (clumped) distribution (Elliott 1977).

As well as these descriptions that are routine in biodiversity conservation, we wanted to address topics such as how the diversity of the biological traits (a functional diversity measure) would be related to that of the genera (a structural diversity measure). For this purpose, Principal Component Analysis (PCA) served to screen correlation circles (see Chessel et al. 2004) for correlations among multiple, untransformed biodiversity variables, which were subsequently analysed in more detail (if required, after log or square transformation of the data). We used Systat-10 for frequency distributions and regressions.

Results

The database provides many possibilities for assessing taxonomic and biological trait patterns among stream macroinvertebrates that could be relevant for biodiversity conservation. We here provide just a few examples to illustrate this potential.

Taxonomic and biological trait characteristics of the macroinvertebrate communities

Descriptions of community characteristics

Genus richness at the 527 sites ranged from 4 to 93 (median 23) and the cumulative frequency distribution had a long upper tail (Fig. 2a). About 40% of the sites had <20 genera and only ~10% of them had >40; ~90% of the sites had less than ~10% of the total 312 genera. In contrast to that of the genera, the cumulative frequency distribution of the trait category richness (i.e. the number of categories occurring at each site) (Fig. 2a) increased rapidly across the richness range (34–61, median 53). At minimum, >50% of the 61 trait categories occurred at a site, and ~70% of the sites had 45–55 categories. Here and below we refer arbitrarily to low or high

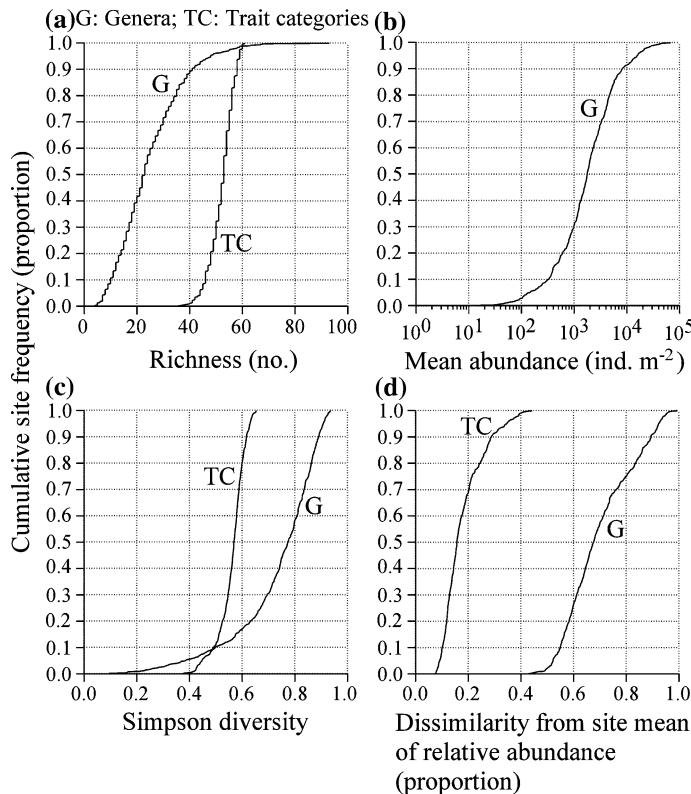


Fig. 2 Cumulative frequency distribution of the 527 sites showing, for genera (G) and trait categories (TC), **(a)** overall richness, **(b)** overall abundance (only shown for genera; see text for explanation), **(c)** Simpson diversity index, and **(d)** Bray–Curtis dissimilarity from the overall site mean (i.e. average of all 527 sites). **(b–d)** using mean absolute or relative abundance at a site

richness (abundance, etc.) in the frequency distributions of Fig. 2 as the 5% of the sites in each tail of the distributions. Sites with low genus richness were typically from small, highland or mountain streams that were either permanent softwater streams of mainland Britain or temporarily dry hardwater streams of the Iberian Peninsula. These genus-poor sites were typically sampled with very small mesh sizes (≤ 0.3 mm), so low genus richness was not a result of sampling with large mesh sizes that potentially missed small genera. Genus-rich sites were typically from permanent streams, both hardwater streams and streams of intermediate hardness, but occurred at all stream sizes and altitudes, and in many biogeographical regions. Among the 5% of the sites with low trait richness were 9 of the 10 Caucasian sites. Other sites with low trait richness were typically from permanent, small softwater streams in highlands. Sites with high trait richness were typically from permanent, lowland hardwater streams of all sizes, including many lake outlets.

Overall, the mean abundance of the genera at the sites ranged from 7 to 67,720 individuals m^{-2} (median 1,770). About 30% of the sites had a mean abundance of $< 1,000$ individuals m^{-2} , and ~10% of the sites had a mean abundance of $> 10,000$ individuals m^{-2} (Fig. 2b). Low abundances were typical for small, permanent or temporary, often softwater, highland or mountain streams, and sites from the Italian

peninsula biogeographical region (which included Corsica and Sardinia) were over-represented. These low-abundance sites were typically sampled with small mesh sizes ($>0.3\text{--}0.5$ mm), so low overall invertebrate abundance was again not a result of sampling with large mesh sizes that potentially missed small individuals. High abundances were also typical for small stream sites, but these were permanent ones and in both lowlands and highlands (and of all types of water hardness).

The Simpson diversity index for the genera ranged from 0.09 to 0.94 (median 0.77), with ~20% of the sites having an index <0.6 and ~10% of them >0.9 (Fig. 2c). For the trait categories it had a narrower range (0.37–0.65, median 0.57) and ~70% of the sites had an index of ~0.5 to ~0.6 (Fig. 2c). The frequency distributions of the Simpson index differed between the genera and the trait categories (Fig. 2c) as clearly as did the richness distributions (Fig. 2a), but for the genera, the Simpson index had a considerably longer lower tail (Fig. 2c) than it did for the richness (Fig. 2a). Small stream size was the only environmental characteristic typical of sites with low Simpson genus diversity indexes; sites with high indexes were also typically from small streams, which also were usually permanent streams in the highlands or mountains. Small permanent stream sites typically had low Simpson trait diversity indexes, and small or intermediate-sized hardwater sites in both lowlands and highlands typically had high diversity.

The dissimilarity of the relative genus abundance at the 527 sites from the overall site mean ranged from 0.43 to 0.99 (median 0.68) and was >0.6 for ~75% of the sites (Fig. 2d). In contrast, the dissimilarity of the relative trait category abundance from the site mean was much lower (range 0.07–0.44, median 0.16) and ~70% of the sites had a dissimilarity <0.2 (Fig. 2d). For the genera, the least dissimilar sites were typically from small permanent streams of mainland Britain, which had no other distinct environmental characteristics; the most dissimilar sites, however, were not only from small streams, but typically also from temporarily dry hardwater streams in both the lowlands and highlands of the Iberian Peninsula. For the trait categories, the least dissimilar sites included no large rivers and, except for being permanent, had no other distinct environmental characteristics; the most dissimilar sites were typically from permanent, small lowland and highland streams, both hardwater streams and streams of intermediate hardness.

Relations among community characteristics

The correlation circle obtained by PCA (Fig. 3a) indicated that the untransformed taxonomic (genera) and biological (trait categories) characteristics of the communities at the 527 sites were correlated in pairs for richness, Simpson diversity, and the dissimilarity of the relative abundance from the overall site mean, whereas the mean abundance at the sites was less correlated to these pairs of variables. Among the pairs, richness and Simpson diversity were positively correlated (both positioned on the negative side of the axis noted F1 in Fig. 3a), whereas the dissimilarity (positioned on the positive side of the F1 axis) was negatively correlated to the former. Thus, high richness and Simpson diversity of genera and trait categories at the sites were associated with low dissimilarity to the mean relative abundances at the sites.

A more detailed analysis of the paired correlations indicated by Fig. 3a showed that the trait category richness increased rapidly with increasing genus richness at genus-poor sites and levelled off near ~30 genera per site (Fig. 3b). In contrast, the relation between trait category and Simpson genus diversity was linear (Fig. 3c) with

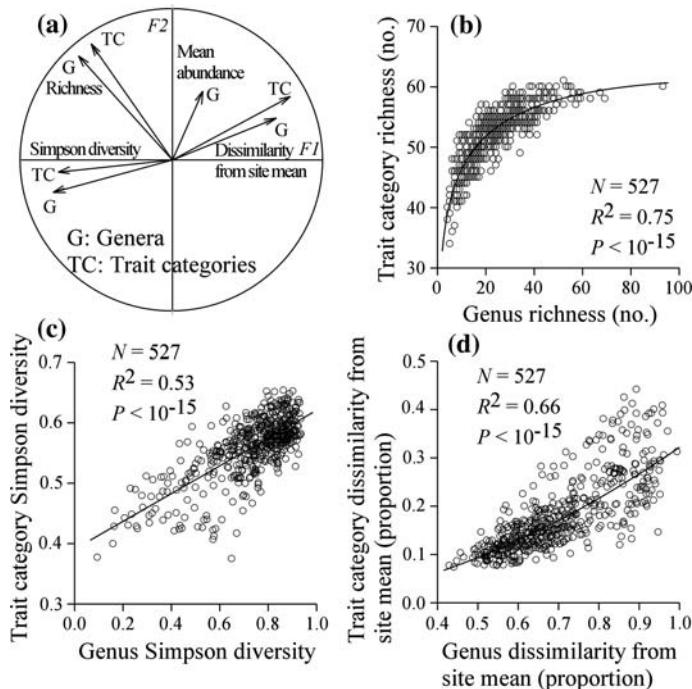


Fig. 3 (a) Correlation circle obtained for the 527 sites by Principal Component Analysis (PCA) among the untransformed variables described in Fig. 2 (the first axis [F1] explained 45.9% and the second axis [F2] 21.1% of the variance); long vectors in the same direction indicate positive correlations among variables, whereas long vectors in the opposite direction indicate negative ones. Also shown are three more detailed relations between trait categories and genera for (b) richness, (c) Simpson diversity, and (d) Bray–Curtis dissimilarity from the overall site mean. See Fig. 2 for further details

a slope (± 1 SE) distinctly <1 (0.23 ± 0.01). Finally, the dissimilarity from the mean relative abundance of the trait categories at all sites increased in a power function in relation to that of the genera (Fig. 3d).

Characteristics of genera and biological traits

Descriptions of genus and trait characteristics

The proportional site occurrence of the 312 genera ranged from 0.0019 (occurrence at 1 site) to 0.88 (median 0.03) and ~80% of the genera occurred at <10% of the sites (Fig. 4a). In contrast, ~70% of the 61 trait categories occurred at >80% of the sites (Fig. 5a; range of proportional occurrence 0.06–1.00, median 0.99). Among the 39 genera occurring at a single site were 9 Coleoptera, 6 Trichoptera, 5 Odonata, 4 Plecoptera, 3 Diptera, and 12 from other groups (e.g. Bivalvia, Hirudinea, Hymenoptera) (see Table 3 for some examples). Among the 15 most frequently occurring genera 14 were insects (Table 3). Among the six least frequently occurring trait categories were those describing size extremes (small or large maximum size, Table 4). Twenty trait categories occurred at all 527 sites (see Table 4 for some examples).

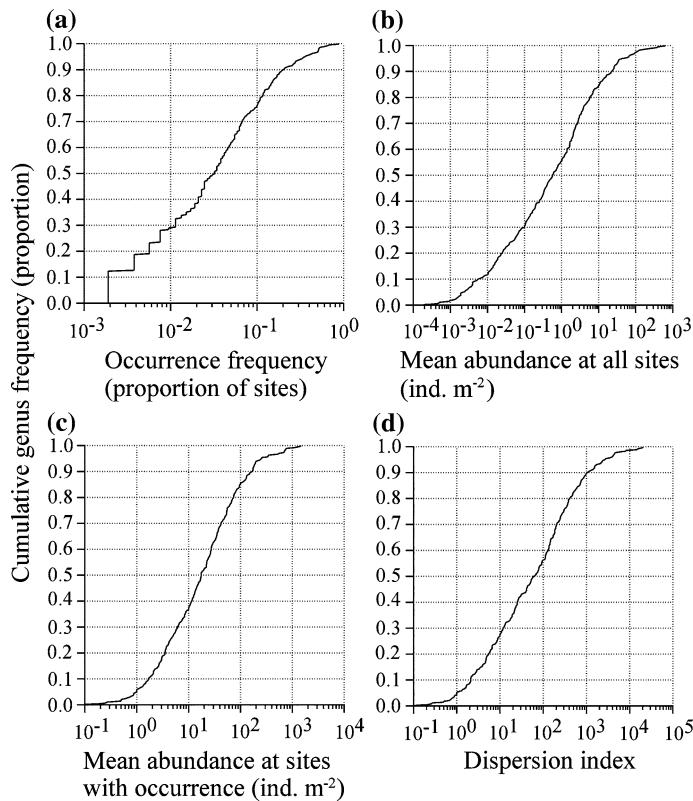


Fig. 4 Cumulative frequency distribution of the 312 genera at the 527 sites showing (a) occurrence frequency, (b) mean abundance at all sites, (c) mean abundance at the sites where they occurred, and (d) dispersion index. See Fig. 2 for further details

The mean abundance of the genera at all sites ranged from 0.0002 to 618 individuals m^{-2} (median 0.57) and ~85% of the genera had a mean abundance <10 individuals m^{-2} (Fig. 4b). Given that several genera may exhibit the same trait category, the mean abundance of the trait categories at all sites (weighted by the number of individuals m^{-2} , see methods section) was higher than the abundance of the genera, ranging from 0.66 to 2,661 (median 409). About 70% of the trait categories had a mean abundance (weighted) of <1,000 (Fig. 5b). Among the 15 least abundant genera nine were insects; 11 insect genera were among the 15 most abundant genera (Table 3). The six least abundant trait categories again included the extreme maximum sizes (Table 4).

The mean abundance of genera at only the sites where they occurred ranged from 0.10 to 1,487 individuals m^{-2} (median 17.5) with ~40% having a mean abundance of <10 individuals m^{-2} (Fig. 4c). Given that so many trait categories occurred at so many sites (Fig. 5a), the frequency distribution of the mean abundance at the sites where they occurred (Fig. 5c, range 3.8–2,661, median 417) resembled the distribution of their mean abundance at all sites (Fig. 5b). Most of the least abundant genera at the sites where they occurred were also the least abundant overall (Table 3). In contrast, the most abundant genera at the sites where they occurred differed more

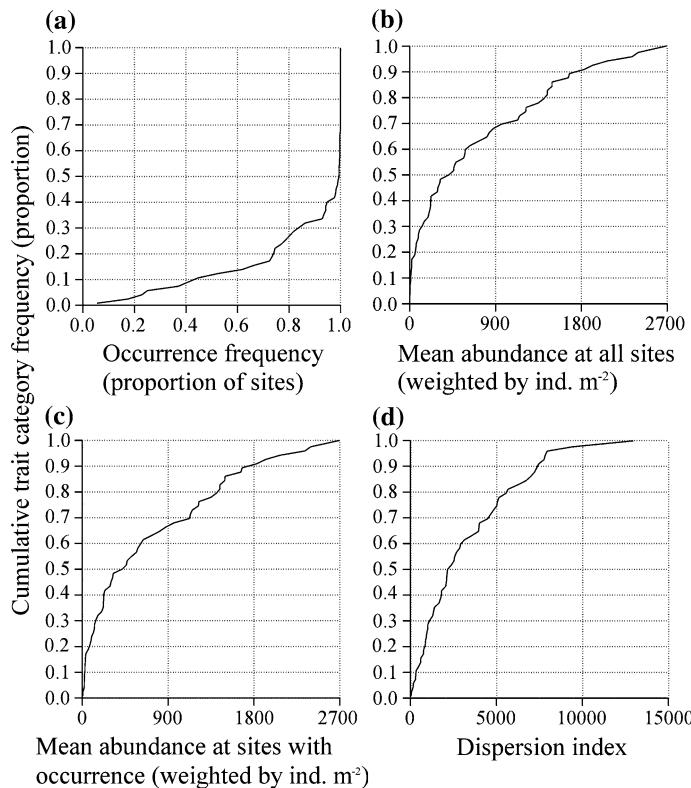


Fig. 5 Cumulative frequency distribution of the 61 trait categories at the 527 sites showing (a) occurrence frequency, (b) mean abundance at all sites, (c) mean abundance at the sites where they occurred, and (d) dispersion index. See Fig. 2 for further details

from the most abundant genera overall (Table 3). Among the six least or most abundant trait categories at the sites where they occurred, all but one were also the least or most abundant at all sites (Table 4).

About 95% of the genera had a dispersion index >1 , often $>>1$ (Fig. 4d, range 0.10–20,023, median 61), i.e. most genera had a contagious (or clumped) distribution. Likewise, all trait categories had a clumped distribution (Fig. 5d), although the higher values for the trait categories (range 17–12,851, median 2,139) were lower than for the genera. Most of the least or most abundant genera at the sites where they occurred also had the lowest or highest dispersion index, respectively (Table 3). From the six least or most abundant trait categories at the sites where they occurred, 5 or 3, respectively, also had the lowest or highest dispersion index (Table 4).

Relations among genus or trait characteristics

The correlation circle obtained by PCA (Fig. 6a) on the untransformed characteristics of the 312 genera indicated that occurrence and mean abundance at all sites were one correlated pair, and mean abundance at the sites where they occurred and dispersion index were another correlated pair. More detailed analysis of these

Table 3 The 15 genera (number arbitrarily selected) in the lower and upper tail of each of the frequency distributions (Fig. 4) of occurrence (O), mean abundance at all sites (MA), mean abundance at sites where they occurred (MAO) and dispersion index (DI). In total, 39 genera (not all included here) occurred only at one site

Lower tail

Porifera: *Heteromyenia* (O, MA, MAO, DI)

Gastropoda: *Anisus* (O, MA, MAO, DI), *Bythiospeum* (O, MA, MAO, DI), *Hygrobia* (O, MA, MAO, DI), *Segmentina* (DI)

Hirudinea: *Dina* (MAO), *Haemopsis* (O, MA), *Hirudo* (MAO, DI)

Decapoda: *Astacus* (O, MA, MAO, DI)

Odonata: *Brachytron* (MAO), *Diplacodes* (O, MA, MAO, DI), *Enallagma* (O, MA)

Heteroptera: *Callicorixa* (O, MA, MAO, DI)

Coleoptera: *Donacia* (O, MA, DI), *Eretes* (O, MA, MAO, DI), *Hydaticus* (O, MA, MAO, DI), *Laccornis* (O, MA, MAO, DI)

Plannipennia: *Sisyra* (MA, MAO, DI)

Trichoptera: *Ironoquia* (O, MA, MAO, DI)

Upper tail

Gastropoda: *Ancylus* (O, MA, DI), *Mercuria* (MAO, DI), *Potamopyrgus* (MA, MAO, DI), *Pseudamnicola* (MAO)

Bivalvia: *Dreissena* (MAO, DI)

Amphipoda: *Echinogammarus* (MA, MAO, DI), *Gammarus* (MA, MAO, DI)

Ephemeroptera: *Baetis* (O, MA, MAO), *Caenis* (O, MA, DI), *Ecdyonurus* (O), *Ephemerella* (O, MA,

MAO, DI), *Rhithrogena* (O, MA)

Plecoptera: *Amphinemura* (O, MA, MAO, DI), *Chloroperla* (DI), *Isoperla* (O), *Leuctra* (O, MA,

MAO, DI), *Nemoura* (O, MA), *Nemurella* (MAO, DI), *Protonemura* (O, MA)

Coleoptera: *Elmis* (O, MA), *Gyrinus* (MAO, DI), *Limnius* (O), *Ochthebius* (MAO, DI)

Trichoptera: *Hydropsyche* (O, MA), *Micrasema* (MA, MAO, DI), *Neureclipsis* (MAO), *Rhyacophila* (O)

Table 4 The six trait categories (number arbitrarily selected) in the lower and upper tail of the frequency distributions (Fig. 5) of the occurrence (O), mean abundance at all sites (MA), mean abundance at sites where they occurred (MAO) and dispersion index (DI). In total, 20 trait categories (not all included here) occurred at all sites. See Appendix 1 for a complete list of traits and their categories

Lower tail

Maximum size (mm): ≤2.5 (O, MA, MAO, DI), >40–80 (O, MA, MAO), >80 (O, MA, MAO, DI)

Reproduction: free clutches (MAO, DI)

Mechanisms for resistance against unfavourable conditions: using refuges to resist desiccation during droughts (O, MA)

Locomotion and substrate relation: flier (DI), almost permanently attached (O)

Food: vertebrates (MA, MAO, DI)

Feeding habits: parasite or parasitoid (O, MA, MAO, DI)

Upper tail

Maximum size (mm): >5–10 (O, MA, MAO, DI)

Life cycle duration (yr): ≤1 (O, MA, MAO)

Potential number of reproduction cycles per year: <1 (DI), 1 (O, MA, MAO)

Reproduction: ovoviparity (DI)

Mechanisms for resistance against unfavourable conditions: diapause or dormancy (DI), none (O, MA, MAO, DI)

Respiration technique: gill (O, MA, MAO)

Locomotion and substrate relation: crawler (O, MA, MAO, DI)

paired correlations showed that both followed a power function. Log–log plots illustrate clearly that site occurrence of the genera increased highly significantly with their mean abundance at all sites (Fig. 6b) and that the dispersion index of the genera

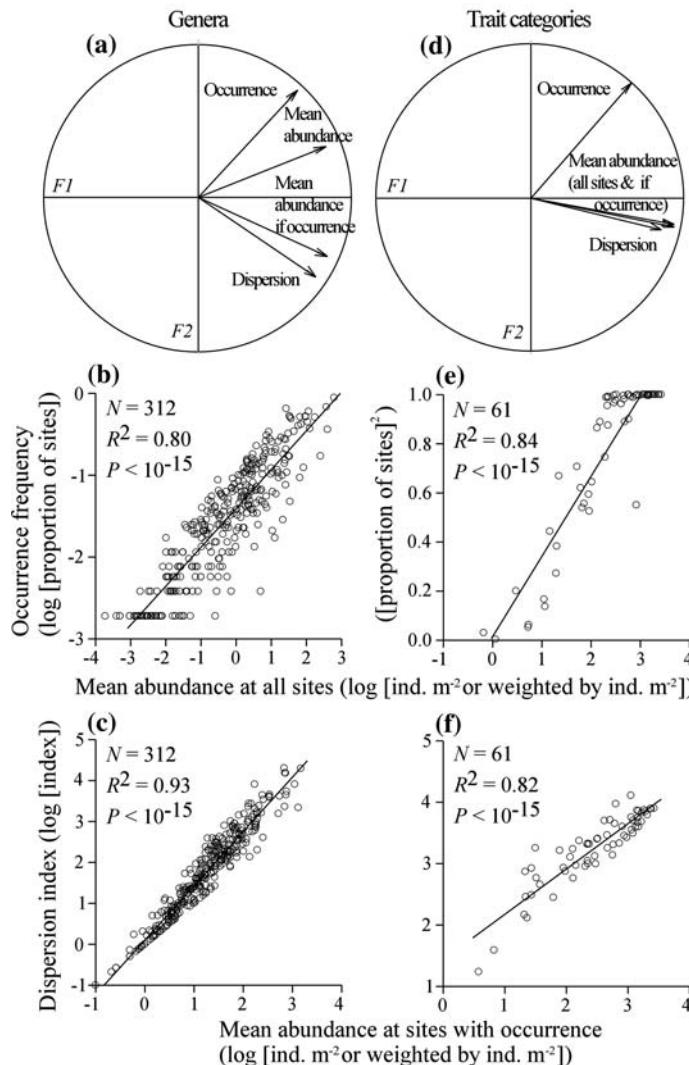


Fig. 6 Correlation circle for (a) the 312 genera and (d) 61 trait categories at the 527 sites obtained by PCA among the untransformed variables described in Figs. 4 and 5 (variance explained by the first and second axes: [a] F1: 77.2%; F2: 15.9%; [d] F1: 64.0%; F2: 23.9%). Two more detailed relations within (b, c) genera or (e, f) trait categories between occurrence frequency and mean abundance at all sites (b, e) and between dispersion index and mean abundance at the sites where they occurred (c, f). See Figs. 3, 4, and 5 for further details

increased highly significantly with their mean abundance at the sites where they occurred (Fig. 6c).

For the 61 trait categories, PCA on their untransformed characteristics indicated that occurrence at the 527 sites was separated from the other three variables that formed a correlated group (mean abundance at all sites, mean abundance at the sites where they occurred, dispersion index, Fig. 6d). More detailed analysis of a potential

correlation between occurrence and mean abundance showed that the square of the trait category occurrence increased highly significantly with the log of the mean category abundance at all sites (Fig. 6e). In comparison, as for the genera, the dispersion index of the trait categories increased highly significantly with the mean abundance at the sites where they occurred, following a power function.

Discussion

Taxonomic and biological trait characteristics of the macroinvertebrate communities

The most genus-poor sites often had <10 genera. These sites were typically from mainland Britain or the Iberian Peninsula, the two regions with by far the most data. Thus, the probability that sites from these two regions appeared by chance among the most genus-poor sites was greater than for other regions. However, the environment of these genus-poor sites provided additional explanations of this relatively low biodiversity. The genus-poor British sites were typically from softwater streams. Soft water affects the occurrence of molluscs and crustaceans (because of their high demand for calcium, Ward 1992) and leeches (typically abundant leech genera suck the blood of molluscs, Elliott and Mann 1979). Thus, all three groups disappear if the water is too soft (Allan 1995). In addition, low calcium levels affect leaf litter decay caused by microorganisms so that this food resource for shredding invertebrates is of lower quality than in hardwater streams (Suberkropp 2001). Thus, softwater conditions were a possible reason for the relatively low genus richness of sites from mainland Britain. In contrast, the genus-poor Iberian sites were typically from hardwater streams. However, these sites were often from temporary (completely dry) streams; such temporary flow imposes such rigorous environmental conditions that typically only specialized taxa can cope with it (Williams 1987). Correspondingly, the most genus-rich sites were typically from permanent streams of high or intermediate hardness.

Compared to generic richness, trait category richness varied little across sites. Given that trait richness was correlated to the rather variable genus richness, one would expect more variation in the former than is apparent in Fig. 2a. However, detailed analysis of this relationship showed that trait richness rapidly increased with genus richness among genus-poor sites but then levelled off. In addition, the scatter in Fig. 3b shows that the most genus-poor or genus-rich sites (and their typical environmental conditions) were not necessarily the poorest or richest in trait categories.

The relatively stable trait richness across the 527 sites corresponded to the overall trait patterns for primarily temperate climate streams (Statzner et al. 2004) and for the least human-impacted large (≥ 40 m wide) European river sites (Statzner et al. 2005). Likewise, the biological traits of benthic macroinvertebrate communities in Californian streams vary little and exhibit seasonal stability, despite high seasonal variation in abundance and taxonomic composition of the communities (Bêche et al. 2006). These relatively stable trait patterns are not well understood, although Statzner et al. (2004) suggested that they might reflect the uniform action of local physical factors that affect many traits in a similar way across large geographic areas. Furthermore, different freshwater genera can have similar biological traits even if they belong to different higher systematic units (Usseglio-Polatera et al. 2000), which would contribute to this stability.

Mean abundance varied greatly across sites and genus richness and mean overall abundance were not closely correlated. This was surprising, as the taxonomic richness of stream invertebrates typically increases with the individuals or the area censused, although deviating patterns have occasionally been observed (e.g. Voelz and McArthur 2000).

The differences in the frequency distribution between the Simpson genus diversity index and genus richness related simply to the weighting of the taxonomic units in the calculation of the Simpson index. Consequently, the sites with the lowest and highest Simpson indexes differed in their environmental conditions from the most genus-poor or genus-rich sites. For the trait categories, the similar shape of the distribution curves for the Simpson index and richness related to the relatively invariant occurrence of many categories at many sites and the elevated dominance of a single category (or a few categories) within most traits (see Fig. 3 in Statzner et al. 2004). As a consequence, the trait category Simpson indexes increased only marginally over the greater range of the Simpson genus diversity indexes.

Although both of the most heavily sampled regions had a similar number of sites in the database, genus abundances at many British sites were more similar to the mean genus abundance at all sites, while those at many Iberian sites were less similar, suggesting once more the possible effect of temporary flow in the Iberian sites (see above). Compared to the genera, trait composition at individual sites was more similar to the mean category abundance at all sites (see above for discussion of trait stability). Given that the overall site mean included all genera and trait categories, higher genus and trait diversity at a site made it more similar to this mean.

Implications of community patterns for biodiversity conservation

In the context of biodiversity conservation, our analyses of the taxonomic characteristics of the sites provided no new general insights. As usual, few sites were so-called biodiversity hotspots but a database with a better regional coverage would enable the identification of European conservation hotspots for stream invertebrates using approaches that have been applied, for example, to mammals (Freitag et al. 1997), birds (Lei et al. 2003) and butterflies (Werner and Buszko 2005). Given that our database includes information on invertebrate abundance and not just occurrence (cf. <http://www.faunaeur.org/>), methods used in the abundance assessments, and several site characteristics, it could provide complementary information to identify conservation priorities. Thus, better regional coverage and public access should be helpful for those working in the field.

Concerning conservation of trait biodiversity, our analyses indicated that the biological trait composition was relatively similar across Europe despite considerable taxonomic differences among the sites. This suggests that invertebrate communities, living in systems typically driven by harsh physical factors (e.g. Ward and Tockner 2001), represent an extreme case, as predicted by the biological insurance hypothesis for biodiversity (Naeem and Li 1997). Thus, this high redundancy (in the sense that many taxa have similar biological traits) may enhance the functional or biological stability of stream invertebrate communities (see Naeem and Li 1997) even if their taxonomic biodiversity cannot be conserved.

A major cause of this trait similarity could be that abiotic factors that lead to trait composition of stream invertebrate communities being more similar are more important than biotic, internal community factors (e.g. asymmetric competition

among taxa) that make their trait composition less similar (Statzner et al. 2004). However, until recently, there was more evidence for the action of biotic than abiotic factors on the trait composition of other community types (Weiher and Keddy 1995). Nevertheless, several studies have now shown that abiotic factors may predominate in affecting the trait composition of other community types so that their traits are relatively similar, for example in higher plants (Tofts and Silvertown 2000). Furthermore, changes in trait patterns, although clear, can be relatively weak (in terms of quantities) in relation to, for example, fishing pressure on marine fish (Jennings et al. 1999), fragmentation and other disturbances of terrestrial beetle habitats (e.g. Ribera et al. 2001) and physical environmental characteristics of stream fish (e.g. Mérigoux et al. 2001). Finally, of the more than 100 trait categories assessed in a study of bird communities (Bournaud 1994), >90% occurred in these communities even if they were very species-poor. Thus, in addition to our results, there is other evidence showing that it would be generally easier to conserve the diversity of biological traits than that of the many taxa sharing similar traits.

Characteristics of genera and biological traits

Various biological characteristics of the genera had implications for their occurrence, abundance, and dispersion index. For example, of the 312 genera, 25 contained only species that typically occur in other freshwater systems such as lakes or ponds (Illies 1978) and eight of these 25 were among the 39 genera occurring at single stream sites. In contrast, genera occurring at many sites with high mean abundances often had many lotic species, according to Illies (1978), including *Leuctra*, *Nemoura*, and *Protonemura* (Plecoptera) and *Hydropsyche* (Trichoptera). Because predators are usually less abundant than their prey, genera with predatory species, such as *Isoperla* (Plecoptera) and *Rhyacophila* (Trichoptera), among the 15 most frequently occurring genera were not among the 15 most abundant genera. Furthermore, genera with species that occur abundantly in particular habitats, such as *Neureclipsis* (Trichoptera), which inhabits lake outlets (Statzner 1987), were among the 15 genera with the highest abundance at the sites where they occurred. Finally, genera with invasive species, such as *Potamopyrgus* (Gastropoda), *Dreissena* (Bivalvia) and *Echinogammarus* (Amphipoda) (Tittizer et al. 2000), had a high mean abundance at the sites where they occurred and a high dispersion index. This reflects the typical pattern of running water invasions: after arrival, invasive taxa typically dominate the invaded invertebrate community for a certain period, after which this dominance decreases but increases elsewhere in newly invaded communities (Tittizer et al. 1994), as is also typical for invasive taxa of other groups of organisms (Sakai et al. 2001).

Sampling techniques also had implications for occurrence and abundance of the genera. For example, among the genera with low occurrence as well as low abundance at the sites where they occurred was *Astacus*, a native European decapod threatened by the introduction of North American crayfish (Laurent 1997). However, occurrence and abundance of this large crayfish and other large invertebrates may be underestimated in our data, as sampling was typically not focussed on large taxa (see below).

Overall, the relations among the genus characteristics showed that low site occurrence was particularly associated with a low mean abundance at all sites (a trivial pattern), although the data exhibited considerable scatter. The positive relation

between the dispersion index and the mean genus abundance at the sites where they occurred was less scattered and thus more reliable.

Many of the patterns observed in the descriptions of and relations among the biological trait categories related to topics discussed above. Given that so many trait categories were relatively well represented at most sites, the most important topic to discuss is relative rarity (occurrence and abundance of trait categories). Not surprisingly, very small (≤ 2.5 mm maximum body size) and large (>40 mm) so-called “macroinvertebrates” were relatively rare in our data, presumably for methodological reasons. To assess the presence and particularly the abundance of very small invertebrate taxa requires the use of fine meshes (<0.25 mm, Barber and Kevern 1974) and most of our data were collected with meshes too large for this purpose. On the other hand, to collect large, generally less abundant invertebrates in a quantitative way typically requires sampling units of large area (Elliott 1977), which would result in unmanageable numbers of individuals of smaller taxa.

The relative rarity of using refuges (e.g. small crevices) as a mechanism of resistance to dessication during droughts could be related to the fact that ~90% of our sites were permanently flowing streams. In contrast, the relative rarity of parasitism in the communities, particularly if compared to the dominance of parasitic insects in terrestrial invertebrate communities, was less easy to explain and related perhaps to evolutionary obstacles encountered by parasitic insects in freshwater environments (Statzner et al. 2004). Finally, one would expect that an almost permanent attachment to the bottom substrate should be a typical trait within communities that are usually exposed to a unidirectional, often highly variable flow regime, yet this trait category was among the rarest.

Implications of genus and trait patterns for biodiversity conservation

Many genera (39) occurred at only a single site and many more occurred at only a few sites. The risk that these genera could become endangered in stream environments is relatively high. A public database providing this detailed information on the genera concerned would be a particularly appropriate tool for transferring this knowledge to potential users.

The genera that occurred at more sites (>10) had a highly contagious (or clumped) distribution, a pattern that is typical for other groups of organisms and that has important implications for conservation (Gaston 1994). In this context, for each genus with extremely skewed site abundance distributions the few sites (and the environmental site conditions) where they were most abundant could be identified from the distributions.

Good identification tools are an essential prerequisite for reliable biodiversity assessments at the species level, and such tools would be particularly important for genera with a high (ranking in the top 15) site occurrence, a high mean abundance at the sites where they occur, and many lotic European species (arbitrarily set by us to >36 species per genus using Illies 1978). Among the 11 genera meeting at least two of these criteria were 5 Plecoptera (*Amphinemura*, *Isoperla*, *Leuctra*, *Nemoura*, *Protonemura*), 2 Amphipoda (*Echinogammarus*, *Gammarus*), 2 Ephemeroptera (*Baetis*, *Ephemerella*) and 2 Trichoptera (*Hydropsyche*, *Rhyacophila*). Given that these occurred frequently with high abundances and/or have many species, species identifications of aquatic stages of these genera were, are, and will be a major task when assessing the taxonomic biodiversity of a European stream site, especially as

these genera are notoriously difficult to identify to species throughout Europe. Calls for better identification tools for freshwater invertebrates have a long tradition (see Lenat and Resh 2001), yet current biodiversity assessments of aquatic stages of stream invertebrates still suffer from the lack of such tools (e.g. Tixier and Guérolé 2005). Combining a database such as ours with external information on the European species richness of genera (such as Illies 1978) would enable the selection of priority groups for which an improvement of specific identification tools is urgently required.

Finally, our analyses of the characteristics of the biological trait categories indicated no major risk that they could disappear as long as there is not a dramatic loss of taxonomic diversity. If at all, one could be slightly concerned about genera that feed as parasites.

Conclusions

The few examples included in this paper illustrate that the taxonomic and biological information on the benthic stream macroinvertebrates in our database provides a rich source that could be used for biodiversity conservation, particularly as these data could be analysed in many other ways (see introduction) at a regional scale (e.g. Alps versus Pyrenees versus Ireland) and for stream types (e.g. small softwater streams in the mountains versus large hardwater rivers in the lowlands). Beyond its use for biodiversity conservation, the database could serve other purposes. For example, a major thread in ecological research uses biological traits to develop ecological theory (Statzner et al. 2001b), and the assessment of the trait composition of invertebrate communities opens up new perspectives for biomonitoring of stream systems (Bonada et al. 2006). To provide these options, particularly when considering finer scales, such as European regions or particular stream types, the database needs expansion. After consultation with colleagues working on stream invertebrates, we suggest proceeding in a stepwise manner (see Appendix 2) to achieve this expansion and public accessibility.

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Appendix 1

Biological traits and their categories in the database.

- (1) Maximum size (mm): <2.5; >2.5–5; >5–10; >10–20; >20–40; >40–80; >80.
- (2) Life cycle duration (yr): ≤1; >1.

- (3) Potential number of reproduction cycles per year: <1; 1; >1.
- (4) Aquatic stages: egg; larva; nymph; imago.
- (5) Reproduction: ovoviparity; isolated eggs, free (not fixed to a substrate); isolated eggs, cemented; clutches, cemented or fixed; clutches, free; eggs or clutches in vegetation (endophytic); clutches, terrestrial; asexual reproduction.
- (6) Dispersal: aquatic passive; aquatic active; aerial passive; aerial active.
- (7) Mechanisms for resistance against unfavourable conditions: eggs, statoblasts, gemmules; cocoons; using refuges (e.g. small crevices) to resist desiccation during droughts; diapause or dormancy; none.
- (8) Respiration technique: tegument; gill; plastron; spiracle or hydrostatic vesicle (aerial).
- (9) Locomotion and substrate relation: flier; surface swimmer; swimmer; crawler; burrower (epibenthic); interstitial (endobenthic); temporarily attached; almost permanently attached.
- (10) Food: fine sediment and microorganisms; detritus <1 mm; plant detritus \geq 1 mm; living microphytes; living macrophytes; dead animals \geq 1 mm; living microinvertebrates; living macroinvertebrates; vertebrates.
- (11) Feeding habits: deposit feeder; shredder; scraper; filter-feeder; piercer (plants or animals); predator (carver/engulfing/swallower); parasite, parasitoid.

Appendix 2

Regarding further development of the database, the majority of colleagues we consulted for advice agreed to develop the database in two steps. The first step would be to use the database as a collective research tool. For this purpose, the data described herein will be implemented in an operational database by Klement Tockner at the Swiss Federal Institute for Environmental Science and Technology (<http://www.eawag.ch/~tockner/~EuropeanRivers>). Access to this research tool will be provided to potential users who have contributed or will add information to the database. Hopefully, such a collective research tool is sufficiently attractive to others that the coverage of European regions and stream types will be rapidly improved. After this improvement is achieved, the second step would be to convert the database into a user-friendly form enabling all sorts of searches and queries and to link it to other existing biodiversity databases (e.g. <http://www.freshwaterlife.org/>) that are freely accessible to the public.

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Ecotourism disturbance to wildfowl in protected areas: historical, empirical and experimental approaches in the Camargue, Southern France

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Abstract Ecotourism is becoming very popular, especially in protected areas where wildlife concentrate and is easier to observe, but the consequences of associated disturbance have seldom been quantified other than in the short-term, making the sustainability of this activity untested. We combined a historical, an empirical and an experimental approach to assess the long-, medium- and short-term consequences of disturbance to wintering wildfowl (*Anatidae*) in a wetland of international importance in the Camargue, Southern France. In the short-term, disturbance made teal (*Anas crecca*) move away temporarily from observation blinds without leaving the waterbody. Wildfowl fed more after disturbance, disrupting their normal resting activities. In the medium-term, waterbodies with more tourists did not host fewer birds: conversely the most heavily disturbed one hosted the highest wildfowl density. In the long term, wildfowl numbers were not related with the number of visitors. When practiced with appropriate guiding of people, and where appropriate facilities are provided to limit human disturbance as done here, ecotourism may not affect wintering wildfowl other than reversibly in the very short term. The legitimate demand of the public for access, even in fragile protected areas, may therefore be sustainable under some conditions.

Keywords *Anas crecca* · *Anatidae* · Camargue · Ecotourism · Human disturbance · Protected areas · Sustainability · Teal · Wildfowl · Winter

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Introduction

Though its impact on long-term wildlife population dynamics is often difficult to establish (e.g. Cayford 1993; Béchet et al. 2004), recreational human disturbance is well-known for its immediate influence on animal behaviour and distribution (e.g. Boyle and Samson 1985; Davidson and Rothwell 1993; Triplet et al. 2003; Blanc et al. 2006). Among these activities, leisure hunting has early been identified as a major source of disturbance (e.g. Madsen and Fox 1995; Harradine 1998; Madsen 1998a; Tamisier et al. 2003). To counterbalance the negative effects of hunting disturbance, hunting-free refuges or reserves have been set-up in most countries, whose benefits have been clearly illustrated by massive redistributions of individuals from hunted to these non-hunted areas (e.g. Owen and Williams 1976; Guillemain et al. 2002; Mathevet and Tamisier 2002). Elegant experimental work by Madsen (1998b) demonstrated that hunting ban by itself could be sufficient to induce displacement of waterbirds, a result that was not confounded by potential improvement in the carrying capacity of sites linked with reserve management as in earlier studies.

Because they host large concentrations of wildlife, protected areas are also very attractive to ecotourists, which themselves can become a source of disturbance within reserves (Blanc et al. 2006). For the manager, a trade-off between the protection of wildlife and the demand of the public therefore arises (e.g. Dahlgren and Korschgen 1992; Johns 1996). Because reserves are often located on public land, because visits can be a non-negligible source of income and because they can also be the basis for public environmental education, ecotourism in protected areas is generally considered as a legitimate activity, but requires adequate policy and/or management. So far, the incidence of ecotourism disturbance in protected areas has mostly been considered in the short-term, through the immediate disruption of behaviour or escape flights of animals (relatively short-term “effects” of disturbance, as opposed to longer-term “impacts”, Robinson and Pollitt 2002; see also e.g. Klein 1993; Burger and Gochfeld 1998; Mathers et al. 2000). The duration of the effect of disturbance, in terms of time taken by the animals to come back to their initial behaviour, has received less attention (see however Lott and McCoy 1995), and the longer-term incidence of ecotourism on habitat use by animals within a reserve has seldom been analysed (Gill et al. 2001). Proposed management measures to mitigate disturbance are often the creation of buffer zones between people and wildlife, the building of designated paths, fences or observation hides, and the limitation of visitor numbers (e.g. Klein 1993; Carney and Sydeman 1999; Finney et al. 2005). Most reserves have such infrastructures or guide small groups of tourists during visits, assuming that this allows preventing completely or at least limiting potential impact on wildlife. However, the consequences of ecotourism under these conditions has seldom been tested (with the exception of Ikuta and Blumstein (2003) concerning the efficiency of fenced areas to protect wildlife), while most protected areas propose visits for schools or to the broader public for the reasons outlined above.

The aim of the present study was to combine historical, empirical and experimental approaches to determine if the use of hidden paths and blinds to observe the birds, combined with a limitation of tourist numbers and a strict guiding of people are indeed appropriate measures allowing the development of ecotourism within a

protected area while still providing suitable quiet wintering conditions to waterbirds, namely Anatidae (dabbling ducks *Anas* spp. and greylag goose *Anser anser*). Ducks and geese are quarry species in many countries (e.g. Mooij 2005, for the European Union), and are known to react strongly to the creation of reserves (e.g. Owen and Williams 1976; Guillemain et al. 2002; Mathevet and Tamisier 2002). These large concentrations of wildfowl are then very popular with the public.

The study was conducted at the Marais du Vigueirat in the Camargue, Southern France. The Camargue is the most important wintering area for wildfowl in France, being of international importance for many species (i.e. in January 2005, for all six dabbling ducks (*Anas* spp.) that winter in western Europe except Pintail *Anas acuta*, Deceuninck et al. 2006). The Marais du Vigueirat are one of the most important Camargue day-roosts for wildfowl, especially dabbling ducks. They gradually became protected from hunting, and free public visits got banned in most of their area over the last 20 years (Mathevet and Tamisier 2002), while guided tours in observation hides and paths hidden to the birds through adequate management (tree hedges) and infrastructures (observation blinds) were developed instead.

Combining 15 years of duck counts at three distinct waterbodies of the site and censuses of the number of tourists at each of these over 10 years, the first aim of this study was, through a historical long-term approach, to determine if any sign of potential limitation of duck numbers could be attributable to the development of ecotourism at the scale of the site and, more precisely, if waterbodies visited more often over a long period were eventually hosting fewer birds than more quiet ones.

The second objective was to rely on traditional empirical methods to determine the effect of tourist visits on the average spatial distribution, numbers and behaviour of wildfowl at three waterbodies with contrasted average frequency of visitor disturbance over a wintering season, on days without such visits, trying to determine if ecotourists have lasting effects in the medium-term.

The third objective, combining real guided visits and experimental disturbance, was to determine the short-term effect of ecotourism on wildfowl distribution and behaviour at the most heavily disturbed waterbody of the site, trying to determine how long it takes for birds to come back to their initial distribution and activities after having been disturbed, if such disturbance arose with guided tours in observation blinds.

Methods

Study sites

The Marais du Vigueirat are a 1,000 ha estate gradually bought since 1982 from private landowners by the Conservatoire de l'Espace Littoral et des Rivages Lacustres, the French national body in charge of pre-empting coastline to prevent its urbanisation and ensure its protection in the long-term (Mathevet and Tamisier 2002). The Marais du Vigueirat are located in Arles in the Camargue, Southern France (43°40'N 04°38'E). The Camargue is the most important wetland for wintering Anatidae in France (see above), and within the Camargue the Marais du Vigueirat is a site of international importance for wintering wildfowl (regularly more than 20,000 wintering individuals; G. Massez personal communication). Because

they frequently host more than 10,600 wintering teal *Anas crecca* (the Ramsar threshold for that population, Delany and Scott 2002) on a rather small area, the Marais du Vigueirat are also of international importance for that species alone, and are the most densely used wetland by teal in France. It is however important to note that duck numbers at the Marais du Vigueirat built up at the expense of other traditional Camargue day-roosts (Mathevet and Tamisier 2002). This suggests that birds potentially have the choice between roosts within the Camargue, a prerequisite for studying the potential impact of ecotourism (which would be meaningless if birds had no other option than to rest at the Marais du Vigueirat whatever their level of disturbance). Forty-five percent of teal wintering in the Camargue spend the daylight hours in unprotected day-roosts (Tamisier and Dehorter 1999). Though 26% of these use one single estate where hunting pressure is relatively low, hunting in itself may therefore not be the major factor affecting teal selection of a day-roost (see also Brochet 2006).

The three main waterbodies of the Marais du Vigueirat were considered in the analyses. These have the same broad characteristics in terms of surrounding vegetation (mostly reedbeds, *Juncus* spp. and *Tamarix* sp.), steepness of the banks (always very low) and depth (generally <1 m in deepest parts), but mostly differ in size (Fangassier 55 ha, Baisse des Oies 15 ha and Rizières 3 ha) and their degree of use by tourist visits: Fangassier is an unvisited sanctuary, Baise des Oies is sometimes visited while Rizières is always used by guided tours (see the results section). Because of these contrasted sizes, only bird numbers per waterbody transformed into density per hectare were used in the analyses.

Wildfowl and tourist censuses—“Historical” approach

Ducks and geese have been counted monthly by the managers of the reserve during winter (September–January included) at the three sites from September 1989 to January 2005. There were only four missing counts: October and November 1989, November 1991 and December 2003. Species considered in this study were greylag goose, teal, mallard *Anas platyrhynchos*, shoveler *A. clypeata*, gadwall *A. strepera*, pintail and wigeon *A. penelope*. Earlier studies have demonstrated that susceptibility to disturbance, often measured as flight initiation distance, can be a species-specific trait (e.g. Blumstein et al. 2003; Blumstein 2006; Fernández-Juricic et al. 2006). In addition to running the analyses for all wildfowl together (teal included), we therefore also analysed the consequences of disturbance for teal alone, because teal is often considered to be one of the most susceptible wildfowl species to disturbance (e.g. Tuite et al. 1984 for *A. crecca crecca*; Pease et al. 2005 for green-winged teal *A. crecca carolinensis* in North America) and is also the main species for which the area is important internationally. Annual average teal numbers represented 56% of average total wildfowl counts at the three waterbodies over the 1989–2005 period.

The full dataset was first used to determine potential trends in average annual numbers of wildfowl or teal over years at the scale of the Marais du Vigueirat, pooling data from the three sites each month and averaging monthly data per wintering season. During those years when some counts were missing the average over remaining available monthly data was used instead. Count data satisfied the normality criterion (non-significant Kolmogorov-Smirnov tests at $P = 0.05$) and were analysed with polynomial regression due to non-linearity of the trend over years.

We then used an ANOVA to compare average annual bird densities (nb ha⁻¹, which also were normally distributed) between the three sites, once for teal and once for all wildfowl together. Bonferroni-adjusted *t*-tests at $P < 0.05$ were used for post-hoc pairwise comparison when appropriate. This was done using data from September 1991 onwards only, the date at which major management works ceased. After this date the three wetlands looked like they do today, while their appearance may have been slightly different in 1989–1990.

The total annual number of visitors in winter (September–March included) was also computed for the three sites together, and was normally distributed. Potential trend over years was analysed as before, as were correlations between the number of visitors and the number of teal or all wildfowl together. Due to relatively smaller sample sizes than for bird counts, the average annual number of visitors was then compared with Mann–Whitney *U* test between Baisse des Oies and Rizières (there were no visitors in Fangassier).

Distribution and behaviour of the birds—empirical approach

The distribution and behaviour of the birds on days without disturbance was studied 1 day per week (only weekdays, Saturdays and Sundays were never considered) at each waterbody using scan sampling (Altmann 1974) from week 11–15 October 2004 to week 7–11 March 2005, except when meteorological conditions (heavy wind, or cold conditions when waterbodies were taken in ice) made it impossible. As opposed to sites open to the public with free access, where the number of people is generally greatest on Saturdays and Sundays (e.g. Evans and Warrington 1997), the number of tourist visits here is relatively similar between weekdays and weekends, often limited to one guided tour per day, sometimes two tours on weekends. In total, data were available for 22 weeks at Baisse des Oies, 19 weeks at Fangassier and 18 weeks at Rizières. Scan samples were taken every hour from 09:00 to 16:00 approximately. During each scan, the behaviour, species and position of each bird on the waterbody was recorded. The position was determined after a set of fixed poles erected at 100 m from the hide (distance measured with a range finder, ca. 10 poles per waterbody) before the beginning of the study. Birds were thus assigned to one of the two possible distance classes: 0–100 m or >100 m. Behaviour was distinguished into five main categories: foraging (whatever the foraging method used, from dabbling to upending), comfort (resting and preening), movement (swimming, walking or flying), vigilance (either immobile or overtly vigilant, with the head raised), plus other less common behaviours (comprising essentially agonistic behaviours and sexual displays). Pooling data from all individuals of a scan sample also provided the total number of birds at each waterbody. Because total count data were normally distributed after non-significant Kolmogorov–Smirnov tests, we used ANOVAs to compare average densities of teal and all wildfowl between waterbodies. Replicates were weekly averages, that is we averaged data from all scan samples of each weekly disturbance-free study day per site to avoid pseudoreplication.

We then compared the proportion of birds >100 m between sites to determine if they were more regularly further away at some waterbodies. The proportions of birds engaged in each of the four main behaviour categories (Foraging, Comfort, Movement and Vigilance) were then compared between waterbodies. In both cases (analyses of distribution and of behaviour), analyses were performed first for teal

alone, then for all wildfowl together. Here too data were averaged per study day to avoid pseudoreplication. Proportions were not normally distributed and an arcsin-transformation (Sokal and Rohlf 1995) did not solve the problem, so proportions were analysed using non-parametric Kruskal–Wallis analysis of variance to perform comparisons between waterbodies, followed by Mann–Whitney pairwise comparisons where appropriate. Percentages are used in the text, tables and figures to ease reading.

Confounding factors

Studies of disturbance often suffer from not considering potentially confounding factors that may affect subject animals' behaviour and distribution (Gill and Sutherland 2000; Gill et al. 2001). We here considered two main confounding factors: food availability and predation risk.

Winter food of teal and mallard, the other most abundant wintering dabbling duck at the Marais du Vigueirat, mostly consist of seeds of natural plants (this is also the case, though to a lower extent, for other dabbling duck species; Green et al. 2002). We therefore sampled seeds at each of the three waterbodies, with 10 replicates per class of distance (0–50 m, 50–100 m, >100 m), once at the beginning (November 2004) and once at the end of the season (February 2005). Two replicates from Fangassier could not be analysed properly, reducing sample size to 58 there. Each replicate was a core of sediment 10 cm long, 7.2 cm in diameter. Samples were sieved (mesh size 0.3 mm, the minimum inter-lamellae distance in a dabbling duck bill, i.e. the smallest size of particles a dabbling duck can retain when filtering the sediment for food, Thomas 1982) and hand-sorted in the laboratory under a binocular microscope. Seeds were then counted per species and the total dry weight per replicate for each species was determined after a reference table (Arzel et al. in press). We compared the average biomass densities of seeds ($\text{g dry weight m}^{-2}$) between the two sampling occasions per site with Student's *t* tests, then used ANOVAs to compare average biomass densities between the three waterbodies. Biomass densities were Log-transformed prior to these analyses, which allowed meeting the normality criterion (non-significant Kolmogorov–Smirnov tests).

Diurnal predation risk was measured as the frequency of fly-overs by raptors, mostly Marsh Harrier *Circus aeruginosus*. Each study day the occurrence of any of such predators was continuously recorded, from morning to evening (see also Fritz et al. 2000). This was measured on all days (i.e. with or without human disturbance) to increase sample size, considering that since both human visits and raptor patrols were discrete and short-termed events, human disturbance should not affect the average daily frequency of fly-overs significantly. In total, sample sizes (i.e. number of daily frequencies) were 42 at Rizières, 26 at Fangassier and 31 at Basse des Oies. Average frequencies were compared between sites with ANOVAs and post-hoc tests when appropriate, again after Log-transformation, which normalized the data (non-significant Kolmogorov–Smirnov tests).

Short-term effects of tourist visits—empirical and experimental approaches

The aim of this last part of the study was to determine, on days with tourist visits, the immediate effect of these on the total number, behaviour and distribution of the

birds, and whether these potential effects lasted for some time. This short-term analysis was conducted at Rizières, the most regularly disturbed of the three sites. In order to do so, on days with disturbance the frequency of scan sampling was increased to one every 15 min during 2 h after the visit, which lasted 10 min approximately. All visits at this hide were guided by a member of the reserve staff, and arrangements were taken so that visits were generally around 11:00. One shortcoming of many field studies of disturbance is that the observer relies on incidental disturbance events, i.e. these cannot be manipulated (Cayford 1993). This was the case in our study, where there were only 16 study days with visits at Rizières over the winter. We therefore relied on an experimental approach in addition to real tourist visits to increase sample size. On 7 days with no tourist visits at Rizières (never more than 1 day per week), we played a cassette where the background noise of a group of people in a closed room was recorded. We adjusted the sound level so that it was similar to the ear to the average noise made by a tourist visit, and played the cassette for exactly 10 min, the cassette player being in the hide and facing the waterbody through an opened window, therefore apparently similar conditions to a real visit. Only the noise made by people was simulated, since real tourist visits were in hides, therefore probably hardly visible to the birds. We first compared the effects (in terms of bird numbers, behaviour and distribution, as described above) of cassette plays and visits to ensure the former simulated the latter adequately and, since no significant difference but one was observed (see the results section), then pooled the two under a “disturbed day” heading and compared the data with those from days without disturbance.

To measure the immediate effect of visits, we compared the average proportion of teal and all wildfowl engaged in each of the four main behaviour categories (Foraging, Comfort, Movement, Vigilance) as well as average bird numbers and distribution (i.e. proportion of individuals >100 m) during the scan samples 15 min after visits or cassette play and the 11:00 scan samples of days without visits.

To measure the time taken by birds to come back to their initial distribution and behaviour, we then compared the average numbers, behaviour and distribution of birds over all scans within 1 h after visits or cassette play with the average of 11:00 and 12:00 scan samples of days without visits (that is data from the two scan samples of each disturbance-free day were averaged, these average daily values then constituting the replicates for the tests). The same was then done for 2 h after visits or cassette play and 11:00, 12:00 and 13:00 scan samples of days without visits.

Total teal or all wildfowl numbers did not follow a normal distribution at this time scale for this site, nor did the proportion of individuals in the two classes of distance or behaviour (Kolmogorov–Smirnov tests, all $P < 0.05$). The effect of the visits (real guided one or simulated) on bird numbers, distribution and behaviour was thus analysed using Mann–Whitney pairwise comparisons. Percentages are used in the text, tables and figures to ease reading.

Results

Wildfowl and tourist counts

Changes in both teal numbers and the total number of wildfowl at the three waterbodies across time were well fitted by type II polynomial regressions: numbers

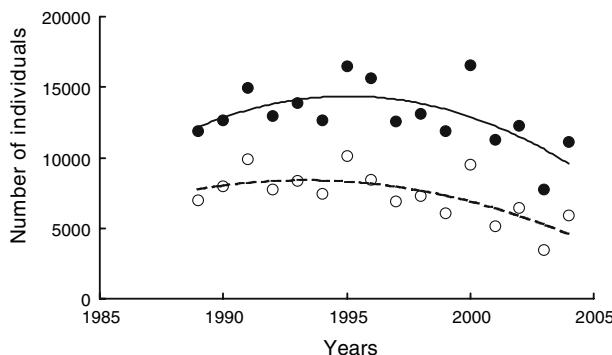


Fig. 1 Changes in teal (white circles, dotted curve) and all wildfowl (black dots and black curve) total numbers across years at the three waterbodies (years refer to the beginning of each wintering season, i.e. 1989 is for winter 1989–90). Equations of regressions are $Y = -33.49X^2 + 356.65X + 7449$ and $Y = -59.77X^2 + 842.56X + 11394$ for teal and for all wildfowl, respectively)

increased slightly from the beginning of the counts until the middle of the 1990s, and decreased since then ($r^2 = 0.47$, $df = 13$, $P = 0.0166$ and $r^2 = 0.42$, $df = 13$, $P = 0.0299$ for teal and for all wildfowl, respectively; Fig. 1). The average density of teal did not differ significantly between the three waterbodies ($F_{2,39} = 3.22$, $P < 0.0506$), due to large variances, though Rizières tended to have a slightly higher number of teal per hectare than the two others (Fig. 2). When all wildfowl were considered together, the density of birds per hectare differed between the three waterbodies ($F_{2,39} = 9.93$, $P = 0.0003$; Fig. 2), and Bonferroni-adjusted *t*-tests showed that it was significantly higher at Rizières than at Baisse des Oies or Fangassier.

Like bird numbers, changes in the average annual number of winter tourists over years since 1995 were well fitted by a type II polynomial regression ($r^2 = 0.81$, $df = 7$, $P = 0.0029$; Fig. 3). This time the maximum numbers were recorded around year 2000. As a consequence, neither the average annual number of teal nor the average number of all wildfowl together were significantly correlated with the average number of visitors (Spearman rank correlations: $r_s = -0.55$ and $r_s = -0.43$, respectively, both P values >0.05). The mean number of visitors per winter at Rizières was

Fig. 2 Average densities of teal (white columns) and all wildfowl (black columns) at the three waterbodies between winter 1991–92 and winter 2004–05. Vertical bars show standard errors, in all cases the number of data is $n = 14$. See text for statistics

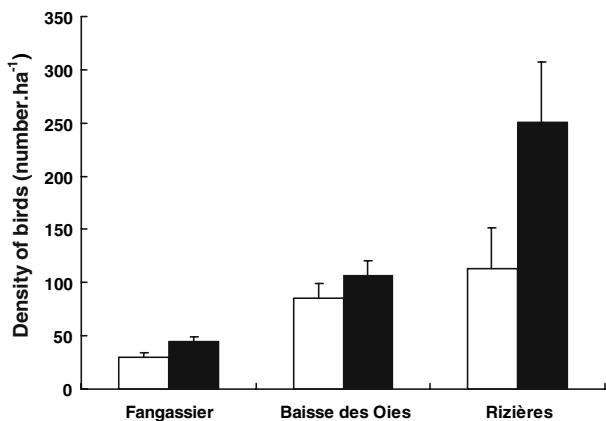
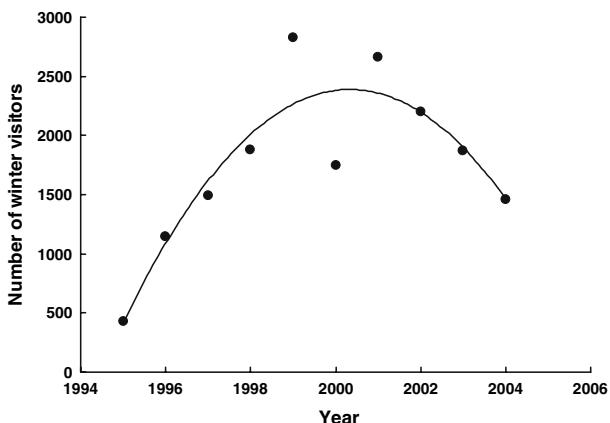


Fig. 3 Changes in the average annual number of winter visitors at Marais du Vigueirat from 1995–96 to 2004–05. Equation for the regression is $Y = -69.12X^2 + 876.17X - 387.52$



1748.2 (± 224.6 SE, $n = 10$), which was significantly higher than the number at Baisse des Oies (866.6 ± 96.4 SE, $n = 10$, Mann–Whitney: $Z = -2.87$, $P = 0.0041$). Fangassier is a sanctuary that is never visited.

Confounding factors

The average biomass density of seeds did not differ between the two sampling occasions at any of the three waterbodies (t tests: all t absolute values < 1.43 , all $P > 0.16$). When data from the two sampling occasions were thus pooled, no significant difference could be detected between mean seed biomass densities of the three waterbodies ($F_{2,175} = 0.41$, $P = 0.6641$). On average at the three study sites seed biomass density was 4.97 ± 0.34 g dry weight m^{-2} SE ($n = 178$). It is true that the power of the test was low (0.1164), so it is likely that potential differences remained undetected due to large variance. However, average seed biomass densities were 4.21, 5.90 and 4.82 g dry weight m^{-2} at Baisse des Oies, Fangassier and Rizières, respectively. Potential differences between sites, if they existed, were thus of limited magnitude and, further, the most heavily disturbed site (Rizières) had an intermediate seed biomass density between the two other waterbodies. It is therefore unlikely that food availability confounded any potential effect of human disturbance on bird behaviour and distribution.

Conversely, the average frequency of fly-overs by raptors was markedly different between the three ponds ($F_{2,96} = 19.03$, $P < 0.0001$), Bonferroni-adjusted post-hoc t -tests indicating that all pairwise comparisons were significant ($P < 0.05$): raptor fly-overs were less frequent at Rizières than at Baisse des Oies, and less so at Baisse des Oies than at Fangassier (Fig. 4).

Average distribution and behaviour throughout a winter

Like for historical data above, Rizières hosted a higher average density of all wildfowl together than Baisse des Oies and Fangassier during winter 2004–05, and there were no significant differences for average densities of teal alone (Table 1). Data for 2004–05 were therefore similar to those over the last 15 years.

Fig. 4 Average frequency of fly-overs by raptors at the three waterbodies from October 2004 to March 2005. Vertical bars show standard errors, numbers in brackets are sample sizes. All three average values differ significantly from each other (see text)

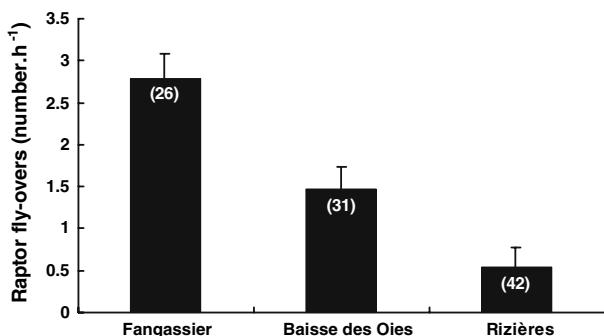


Table 1 Average densities of teal alone or all wildfowl together at the three waterbodies during winter 2004–05

| Fangassier (n = 19) | Baisse des Oies (n = 22) | Rizières (n = 18) | ANOVA | |
|--------------------------------------------------------------------|-----------------------------|----------------------|-------|---------|
| | | | F | P value |
| Teal density (number ha ⁻¹) 12.7 ± 3.1 | 8.9 ± 2.8 | 13.2 ± 3.1 | 0.66 | 0.5227 |
| Density of all wildfowl (number ha ⁻¹) 17.9 ± 5.8 A | 18.9 ± 5.4 A | 46.5 ± 6.0 B | 7.72 | 0.0011 |

Values are means ± SE, values with different letters differed significantly after Bonferroni-adjusted post-hoc t-tests

Teal did not make the same use of the area at the three waterbodies, as illustrated by the significant difference in the relative use of the area further than 100 m away from the hide (Kruskal-Wallis: $H_{2,57} = 14.56$, $P < 0.0001$): Fangassier: $97.07 \pm 4.16\%$ SE, $n = 19$; Baisse des Oies: $94.66 \pm 3.87\%$ SE, $n = 22$, Rizières: $62.59 \pm 4.53\%$ SE, $n = 16$. Pairwise comparisons showed that the relative use of the area >100 m away from the hide did not differ between Fangassier and Baisse des Oies (Mann-Whitney: $Z = -0.10$, $P = 0.9167$), but was higher at these sites than at Rizières (both Z values >3.25, both $P < 0.0012$). Birds therefore relied more on the areas closer to the hide at Rizières than at the two other sites. However, given the differences in size between the three waterbodies, the zone >100 m does not always represent the same percentage of the total area: it actually represented 46.2% of total pond area at Rizières, 89.6% at Baisse des Oies and 92.8% at Fangassier. Based on the comparison of the relative use by teal compared to the relative area it represented (comparison of a single observation with the mean of a sample, Sokal and Rohlf 1995 p. 228), no significant selective use of the area >100 m could be detected at any of the three waterbodies (all t absolute values < 0.87, all $P > 0.05$). Birds therefore apparently distributed according to relative available area, i.e. did not avoid areas closer to the observation blinds.

For all wildfowl together too the relative use of the area >100 m from the hides differed between the three waterbodies (Kruskal-Wallis: $H_{2,59} = 30.19$, $P < 0.0001$). Pairwise comparisons showed that the proportion of birds >100 m did not differ significantly between Fangassier and Baisse des Oies ($97.54 \pm 3.04\%$ SE, $n = 19$ and $97.38 \pm 2.82\%$ SE, $n = 22$, respectively; Mann-Whitney: $Z = 0.80$, $P = 0.4252$),

Table 2 Average percentage of time (\pm SE) spent in the four main behaviour categories by teal or all wildfowl together during winter 2004–05

| | Fangassier | Baisse des Oies | Rizières | Kruskal–Wallis | |
|---------------------|------------------|------------------|------------------|----------------|---------|
| | | | | H | P value |
| Teal alone | | | | | |
| | (n = 18) | (n = 20) | (n = 16) | | |
| Foraging | 7.2 \pm 1.8 B | 9.3 \pm 3.1 B | 40.1 \pm 7.6 A | 10.91 | 0.004 |
| Comfort | 49.9 \pm 6.0 A | 37.6 \pm 4.4 A | 21.8 \pm 5.9 B | 10.97 | 0.004 |
| Movement | 33.9 \pm 5.6 | 38.1 \pm 4.9 | 23.0 \pm 5.4 | 5.72 | 0.057 |
| Vigilance | 8.6 \pm 2.3 | 13.8 \pm 5.2 | 14.5 \pm 7.6 | 2.24 | 0.325 |
| All wildfowl | | | | | |
| | (n = 19) | (n = 22) | (n = 18) | | |
| Foraging | 16.5 \pm 2.3 B | 17.8 \pm 2.2 B | 34.6 \pm 5.6 A | 10.03 | 0.006 |
| Comfort | 50.0 \pm 4.1 | 42.8 \pm 2.1 | 44.8 \pm 5.7 | 4.03 | 0.133 |
| Movement | 26.0 \pm 3.0 A | 30.6 \pm 1.8 A | 13.9 \pm 2.7 B | 17.76 | <0.001 |
| Vigilance | 7.2 \pm 1.8 | 7.9 \pm 1.7 | 6.4 \pm 1.6 | 1.20 | 0.547 |

Results of Kruskal–Wallis analyses of variance are indicated. Values with different letters differed significantly ($P < 0.05$) after Mann–Whitney tests. Numbers in brackets are sample sizes

while values from these two sites were both higher than at Rizières ($55.51 \pm 3.12\%$ SE, $n = 18$, both $Z > 4.66$, both $P < 0.0001$). However, as above based on the comparison of the relative use by wildfowl compared to the relative area it represented, no significant selective use of the area >100 m could be detected at any of the three waterbodies for all wildfowl together (all t absolute values <1.62 , all $P > 0.05$). Wildfowl therefore simply distributed according to available area, not to the position of observation blinds.

Statistics concerning the average time-budget of either teal alone or all wildfowl together are presented in Table 2. In both cases birds spent significantly more time foraging at Rizières than at the other sites, at the expense of comfort activities for teal and at the expense of movement behaviours for all wildfowl together. The average proportion of time spent vigilant did not differ significantly between waterbodies in either teal or all wildfowl.

Short-term effects of tourism disturbance

At Rizières, days with no disturbance, with a guided visit and with the cassette recording being played were first compared with regards to the total number of individuals, the proportion of individuals >100 m from the hide and the proportion of time spent foraging, in comfort, in movement or vigilant, in teal alone then for all wildfowl together, either 15 min, 1 h or 2 h after the disturbance event (or comparable periods of the day on days without disturbance). There were no significant difference ($P > 0.05$) between the three types of days for any of the measured variables or, if some difference was observed, post-hoc pairwise tests did not reveal that data after visits differed significantly from data after playing of the cassette. Data from days with visit and days with a cassette play were therefore pooled under the general “disturbed day” heading below to ease the analysis of the effects of disturbance in general.

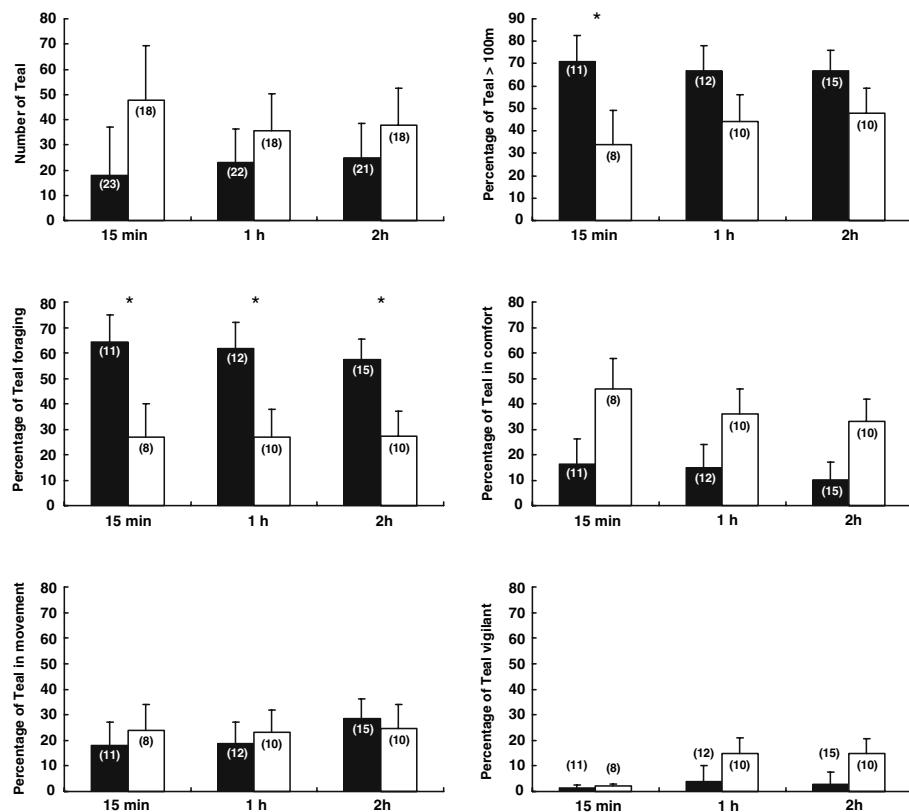


Fig. 5 Average numbers, distribution and behaviour of teal at Rizières on days with (black) and without (white) disturbance. Vertical bars show standard errors, numbers in brackets are sample sizes. Stars represent statistically significant differences after Mann–Whitney tests

For teal alone, there was no significant difference between the number of birds on the waterbody on days with or without disturbance, either 15 min after disturbance or during the following 1 or 2 h. About 15 min after disturbance, there were more individuals >100 m and birds fed more (Fig. 5). When the periods of 1 h or 2 h after the disturbance event were considered instead, the difference in distribution was no longer significant, but teal still fed more on disturbed than on undisturbed days (Fig. 5).

For all wildfowl together, disturbance did not cause a change in total number of birds present or their distribution over the waterbody, neither at 15 min nor during the 1 or 2 h after disturbance, though at 15 min the proportion of birds >100 m was almost significantly higher on days with disturbance ($Z = 1.88$, $P = 0.0603$). Large variance was probably the reason why no significant difference could be detected between days with and without disturbance concerning total bird numbers. Concerning behaviour, birds fed more (though for 1 h the difference was marginally significant: $P = 0.0851$), spent less time in comfort and more time in movement (except for movement at 15 min: $Z = 1.30$, $P = 0.1973$) on days with disturbance than on days without (Fig. 6).

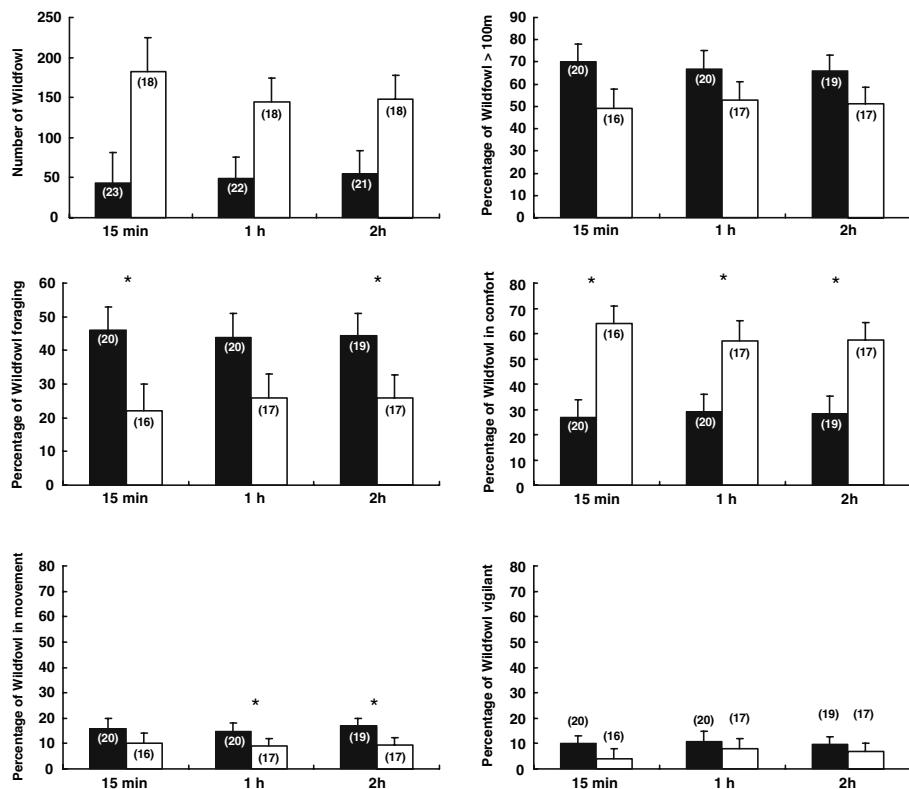


Fig. 6 Average numbers, distribution and behaviour of all wildfowl together at Rizières on days with (black) and without (white) disturbance. Vertical bars show standard errors, numbers in brackets are sample sizes. Stars represent statistically significant differences after Mann–Whitney tests

Discussion

Short-term effects of disturbance: distribution and behaviour of birds after tourist visits

When disturbance occurred, be it real visits or experimental cassette display, teal reacted initially by moving away from the hide for 15 min, then came back to their initial distribution within 1 h, while no birds left the waterbody. This highlights the fact that these ducks probably got accustomed to disturbance to some extent, or that the cost of moving elsewhere was too high. A similar pattern was recorded for all wildfowl species together, though the difference in distribution between days with or without disturbance at 15 min was just above the significance threshold. It is interesting to note that teal reacted more than other wildfowl, as observed in other studies (e.g. Tuite et al. 1984; Pease et al. 2005). These results also support the idea that though the level of susceptibility to disturbance may strongly differ even between closely-related species (Burger and Gochfeld 1998; Rodgers and Schwikert 2002 for waterbirds; Fernández-Juricic et al. 2001 for urban birds), local conditions determine which species of a community are the more likely to react to disturbance

(e.g. classification of waterbird species the most affected by disturbance in Platteeuw and Henkens 1997 as opposed to that in Tuite et al. 1984). In both teal and all wildfowl, a clear effect of disturbance was observed on time-budget, that lasted for a few hours at least: after a disturbance event birds fed more than during corresponding periods of the day when free from disturbance, mostly at the expense of comfort activities (though the difference did not reach the significance threshold in teal alone). The reason why it is feeding activities (rather than vigilance) that increased in the time-budget of disturbed birds is unclear: in many cases an opposite trend of decreased feeding time is recorded following disturbance (Owens 1977; Lott and McCoy 1995; Burger and Gochfeld 1998; White et al. 1999; Duchesne et al. 2000). However, these studies were mainly dealing with animals that were initially foraging before being disturbed, i.e. their main activity was disrupted, as were the comfort activities of our ducks and geese. Disturbance therefore clearly affected, potentially negatively, the behaviour of the birds at our study site. It cannot be excluded that teal and other wildfowl at Marais du Vigueirat increased feeding time after disturbance in order to try to compensate for energy loss related with involuntary movement, just like Mute Swans *Cygnus olor* do as described by Madsen (1998a). However, this would only hold if ducks and geese were able to maintain feeding efficiency after being disturbed, which remains to be proved and would need further work.

To conclude about short-term effects of disturbance, it is clear that ecotourists do have an effect on wildfowl behaviour, and for some species also on their local short-term distribution, even if at our study sites visitors are briefed and guided, and remain in designated facilities. Ducks and geese therefore apparently did not fully habituate to human disturbance at Marais du Vigueirat, even at the most frequently disturbed of the reserve waterbodies.

Medium-term effects of disturbance: distribution and behaviour throughout a winter

The average density of wintering teal alone did not differ between the three waterbodies, while for all species together Rizières hosted the highest density of birds. It is remarkable that Rizières is also the lake with the highest frequency of tourist visits: in the medium term, tourist visits as practiced in Marais du Vigueirat therefore do not seem to prevent the use of wetlands by ducks and geese. Within waterbodies, the distribution of birds was not skewed towards the most distant areas from the hides neither but, conversely, birds appeared to be regularly distributed over the two classes of distances. It is to our knowledge the first time these patterns of distribution (lack of differences between lakes with contrasted disturbance regimes and within lakes in relation to distance from the disturbance source) are demonstrated: on the contrary, abandonment of disturbed wetlands by waterbirds (Evans and Warrington 1997; Madsen 1998b; Marsden 2000; Evans and Day 2002) and more generally under-use by wildlife of areas closer to human activities (Owens 1977; Madsen 1985; Keller 1991; Klein et al. 1995; Gill 1996; Larsen and Madsen 2000; Evans and Day 2001; Lafferty 2001; Taylor and Knight 2003; Finney et al. 2005) are the most commonly documented situations. It is true that visitors are few even at Rizières (13 people per day on average over the last 5 years), and that tourists there are briefed and guided, and remain in hidden paths and observation

blinds, which is likely to reduce disturbance. Tourist disturbance can be much higher and much less regulated at other sites elsewhere, and can therefore potentially have there more serious effects than those described here. As an example for comparison, when testing the effect of varying levels of disturbance on birds flight initiation distances, Webb and Blumstein (2005) used an area where the average instantaneous number of visitors was up to 24 people. However, this was precisely the aim of our work: while most managers suggest that reducing the number of visitors and providing adequate guiding and facilities should be promoted to reduce disturbance, actual disturbance under these conditions had to our knowledge never been tested. Our results suggest that while in the short-term visits may still impact birds distribution and behaviour (see above), such ecotourism policies are indeed a valuable option allowing to prevent medium-term disturbance to wintering wildfowl.

Average time-budgets, on the other hand, differed markedly between the three waterbodies, and surprisingly the main difference was a twice (all wildfowl) or four times (teal alone) higher proportion of time spent foraging at Rizières compared to Baisse des Oies or Fangassier, while Rizières was the most frequently disturbed of the three wetlands on average (time-budgets in this case being recorded on disturbance-free days only). One may consider that this higher tendency to feed at Rizières, at the expense of comfort or movement activities, may therefore be a remnant effect of higher average disturbance (just like foraging is more frequent at Rizières after tourist visits). However, it cannot be excluded that differences in average time-budget are simply reflecting better foraging conditions at Rizières: if this was the case, it is however not through higher food availability, which was observed not to differ between the three study sites. A possible explanation may be linked with the fact that the frequency of disturbance by Marsh Harrier was markedly lower at Rizières, and that this lower predation risk allowed ducks and geese engaging in feeding behaviour more easily, while foraging may globally be a risky activity (especially so for these birds when they forage with the eyes underwater, Guillemain et al. 2001). This hypothesis cannot be properly tested at present, but would be consistent with the marginally significant negative relationship between average daily proportion of time spent foraging by teal and average daily frequency of fly-overs by Marsh Harriers on the 15 days when both could be computed at Rizières (Spearman rank correlation: $r_s = -0.44$, $P = 0.085$). The lower average frequency of fly-overs by raptors at Rizières probably has nothing to do with the frequency of tourists there, but is most likely to be related with the relatively low number of wildfowl present: earlier studies have shown that these raptors patrol less often over waterbodies with fewer ducks and geese (Fritz et al. 2000), as was the case here for Rizières.

Long-term effects of disturbance: wildfowl and tourist counts

Both the annual number of wildfowl (or teal alone) and the average number of tourists visiting the Marais du Vigueirat were well fitted by type II polynomial regressions, but the period of maximum in the curves differed, occurring 5 years earlier for birds than for tourists. The study by Mathevet and Tamisier (2002) demonstrated that the massive increase in wildfowl numbers (especially ducks) at the Marais du Vigueirat during the second half of the 1980's was due to the protection status acquired by the site by that date. Another more recent study showed that trends in teal and all wildfowl at the Marais du Vigueirat were then

strongly correlated with numbers of these birds at the scale of the whole Camargue delta (Blanc 2005) during the 1990–2005 period, so that the patterns observed in Vigueirat were linked with more general factors than just the local number of tourist visits, plus potentially other local management or environmental factors (N. Hecker, personal communication). The reason why the number of visitors also decreased in recent years (i.e. mostly since year 2000) is purely artificial, and is linked with new law regulations over the work of nature guides and wardens, that lead the site to be deliberately closed to the public each year in December and January since year 2000.

In the long-term, there was therefore no apparent contradiction between the development of ecotourism as practiced here and the increasing attractivity of the site for wildfowl (though it is impossible to determine the carrying capacity itself and whether the development of the ecotourism activity impacted the rate of increase in wintering bird numbers). However, the effect of ecotourism at Marais du Vigueirat seems to be limited, since contrary to our expectations the most frequently visited waterbody also had the highest (for all wildfowl together) or a similar (for teal) bird density than the other ones.

Conclusion

Short-term negative effects of human disturbance on animals have been described on many occasions for various species and environmental systems (Boyle and Samson 1985; Dahlgren and Korschgen 1992; Cayford 1993; Klein 1993; Tamisier et al. 2003; Triplet et al. 2003; Blanc et al. 2006). However, without neglecting the ethical problem that disruption of wildlife behaviour may represent, it is clear that conservationists should especially be concerned by those disturbances that affect population dynamics in the long term, rather than by those constraining the behaviour of some individuals for only short periods (e.g. Cayford 1993). However, linking a disturbance event with breeding success and survival several months or years later may be challenging, even more so in migrating animals for which these events may occur several thousands of kilometres apart. In addition to modelling, which may be another way out in this domain (e.g. Gill and Sutherland 2000), long-term studies such as the one we partly relied on may help establishing such links, since one may believe that the use of an area whose disturbance conditions directly affect individual survival and breeding success may decrease over time if animals behave optimally and have alternative options, like here in the Camargue where suitable wetlands are numerous.

Combining different methods allowed us considering the consequences of tourist visits within a protected area at different time and spatial scales: though a traditional short-term with/without disturbance analysis would have suggested that ecotourism as practiced in Marais du Vigueirat does have an effect on wildfowl behaviour and distribution, our results show that there are no visible carry-over effects in the medium or long term. Such a test of the consequences of ecotourism in a protected area shows that if some precautions are taken in terms of limiting the number of visits, guiding of people and provision of adequate facilities, then the opening to visitors can be a sustainable activity within nature reserves.

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The effect of femel- and small scale clear-cutting on ground dwelling spider communities in a Norway spruce forest in Southern Germany

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Abstract. The early effects of femel-cutting (removing 20% of the trees) and small scale clear-cutting on ground-living spiders in a Norway spruce (*Picea abies* (L.) Karst.) forest in Southern Germany were investigated. The study was carried out as BACIP (before and after, control-impact, many paired samplings) study: Spiders were sampled during the pre-treatment year, the year of cutting, and the year after cutting. In total 7101 individuals were sampled, of which 4530 individuals were identified, 4468 were adult and 2633 individuals were juvenile. We identified 107 species, but a single species, *Coelotes terrestris*, dominated the control (spruce stand) comprising up to 49% of the total identified individuals. Clear-cutting changed the species composition in the traps, while the first step in femel-cutting preserved it. The number of individuals of the families Linyphiidae, Amaurobiidae, Agelenidae and Clubionidae decreased drastically within the 2 years after the clear-cutting, while the Lycosidae became numerically dominant in the clear-cut stands. The number of individuals with the following characterisation decreased significantly after clear-cutting: Small (<3.0 mm) and large spiders (>10.5 mm), web builders, ‘forest habitat species’, species favouring hygrophilic to medium moisture conditions, and preferences to live below ground or in and on the moss layer. On the other hand, middle-sized spiders, free hunters, ‘open habitat species’, spiders favouring dry conditions or that are euryoecious, preferring patterns covered by grasses or uncovered patches, increased in number. Clear-cut habitats with dense spruce regeneration showed a delayed and less pronounced response. With femel-cutting, species composition of ground-living spider communities may be preserved during the first step of regeneration of mature forest stands.

Introduction

The Norway spruce stands in Southern Germany, which have largely replaced the original European beech forests, are well known by foresters for their high average annual volume increment (Huber et al. 2004a). However, recently concerns have arisen about possible negative ecological impacts of these uniform even-aged Norway spruce forests. These forests are highly susceptible to the frequent storm events, drought, and bark beetle outbreaks causing

unforeseen fellings, which increase the economic risks for forest managers (Anonymous 2004). Case studies made in some forests of this region show indications of serious ecological problems. Actual difficulties faced are the high nitrogen input (Huber and Kreutzer 2002; Huber et al. 2002; Rothe et al. 2002), soil acidification (Kreutzer 1995; Huber et al. 2004a), nitrate contamination of groundwater resources (Huber et al. 2004b; Rothe and Mellert 2004), and unexpectedly high N₂O emissions from the soils (Butterbach-Bahl et al. 1998). From a biodiversity perspective, these stands often appear uniform, and may have a low value for nature conservation.

One goal of the official forest management administration in Bavaria is to transform these pure coniferous stands into mixed forests. From 1987 to 2002, the proportion of areas with broadleaf trees increased from 22 to 32% (Anonymous 2004). In years to come, more and more conifer rich forests will be converted with efforts focused in the southern part of Bavaria. Therefore, we have studied exemplarily at the Höglwald site the impacts of regeneration on seepage water quality (Weis et al. 2001; Huber et al. 2004b), emission of nitrogen trace gases, and the diversity of different fauna groups before and in the first two years after the felling of the trees (for example Huber and Baumgarten 2005).

There are generally two methods used in this region for stand conversion. Either private forest owners make small clearcuts between 0.5 and 1 ha in size, or the Bavarian state forest administration regenerates the stands with femel cutting. Femel cutting is a relatively unspecific term for a cutting strategy to maintain a ‘continuous covered forest’. Within a time span of 10–15 years single to groups of trees are selectively felled, while the saplings grow under the cover of the remaining stand. The final cutting will be done after the regeneration is established. With clear-cutting, the entire tree layer is removed causing an increase in temperature and decrease in shade (Geiger 1961).

The impacts, opportunities and threats of the two main management options on ecological important values are quite unclear and are, like many other forest practices, largely untested scientific hypotheses (Larsson and Danell 2001; Spence 2001; Siira-Pietikäinen et al. 2003). Femel-cutting or selective cutting is thought to have a lower impact on faunal groups and may serve as a potential tool for maintaining biodiversity in managed forests (Siira-Pietikäinen et al. 2003; Atlegrim and Sjöberg 2004; Huber and Baumgarten 2005). However, until now, studies on the ecological effects of femel-cutting are scarce. Also, data about the response of forest spiders are limited (Pajunen et al. 1995), despite the fact that spiders play a significant role as predators in forest ecosystems (Moulder and Reichle 1972; Buddle et al. 2000), are sensitive to habitat change (Robinson 1981; Riechert and Gillespie 1986; Uetz 1991), have clear taxonomic hierarchy (Duffey 1978), and are easily sampled and identified (Buddle et al. 2000).

In the paper we study the influence of two conversion methods (clear-cutting, femel-cutting) on spider communities. Our hypotheses are:

- (I) Small-scale clear-cuts affect the assemblages of spiders:
 - (a) Species richness increases due to the new structures of the small-scale clear-cut
 - (b) The number of individuals of species typical for open habitats increases
 - (c) The numbers of most forest species individuals decrease, but they are still present on the regeneration sites
- (II) Femel-cutting preserves the original assemblages in the first cutting.

Materials and methods

Site description

The study was conducted at the Höglwald site, which has been a long-term ecological monitoring and experimentation site for more than 20 years with the focus on biogeochemistry and ecosystem research (Kreutzer and Bittersohl 1986; Kreutzer 1995; Butterbach-Bahl et al. 1998; Gessler et al. 1998; Kreutzer and Weiss 1998; Rothe et al. 2002; Huber et al. 2004a, b). The region belongs to the temperate broad-leaf zone, originally dominated by beech. The forest district of the Höglwald (370 ha) is situated in the hilly landscape of Southern Bavaria, 540 m above sea level, about 70 km north of the Alps and 50 km west of Munich (centre) at 11°04' E and 48°17' N. The forest is surrounded by intensively managed farmland (cattle breeding, diary, and corn). The climate is suboceanic. For the period 1984–2001 mean annual precipitation was 933 mm, mean annual temperature 7.7 °C, and the mean number of days exceeding 10 °C mean temperature was 155. During the observation period from 1999 to 2001, the climatic data differed from the long-term means. The mean temperature in this period was 8.2 °C and the mean bulk precipitation amounted to 1161 mm on average. The soil is a parabrown earth (Central European System) (USGS: Typic Hapludalf; FAO: Dystric Cambisol), which is strongly acidified in the topsoil. An organic layer 6–8 cm thick covers the mineral soil. The humus form is moder and the pH values are extremely low with a minimum in the Oh horizon of 2.75 (KCl). The investigated stands are healthy mature Norway spruce plantations, (*Picea abies* (L.) Karst), second generation after beech (*Fagus sylvatica* L.), cultivated in 1910/11 with 3 or 4-year-old plants. The spruce stand is growing vigorously with a high volume increment (Huber et al. 2004a), is full-stocked, and has a closed canopy. The last thinning was performed in 1975. Mosses dominate the ground vegetation.

Experimental treatments and plots

The experimental manipulations involved pre- and post-harvesting assessments. The study can be categorised as a BACIP (before and after, control-impact, many paired samplings) study. A great frequency of before and after

experimental designs are used in water studies and offer a practical alternative for studies where a treatment replication is not possible, but compensation for issues regarding spatial replication is needed (Bennett and Adams 2004). The benefits of these studies have been demonstrated recently in water and bio-diversity studies (Likens 2001; Siira-Pietikäinen et al. 2001, 2003; Huber et al. 2004a, b).

In 1999 the experimental plots were installed prior to the clear-cutting and femel-cutting treatments, which were performed with a harvester in February 2000. Stems including bark were removed and slash remained on the plots. In an area with very uniform stand and site conditions the following treatments were made:

- C: control plot, spruce without cutting (named in other investigations A1)
- F: femel-cutting (0.9 ha), regeneration with planted beech saplings
- CC: small scale clear-cut (1.0 ha) divided into the following two parts
- CCB: clear-cut, regeneration with planted beech saplings (0.5 ha)
- CCS: clear-cut, regeneration with natural or planted spruce saplings (0.5 ha)

Femel-cutting was performed removing 20% of the trees in an area of approx. 0.9 ha, followed by planting beech saplings. The clear-cut was divided into a part regenerated with beech and a part regenerated with spruce. Five-year-old saplings (beech or spruce) were planted in March 2000. On a small part of the CCS, 5–10-year old spruce trees are growing, that originated from seedlings of the mature stand (natural regeneration). Fences and small roads separate the experimental treatments. The femel-cutting treatment is situated in the centre, 250 m NE is the control, and 150 m SE the clear-cut treatment.

Spiders were collected at each treatment (C, F, CCB, CCS) with a combination of pitfall (ten traps) and emergence traps (six traps), as was done previously in the study of Ratschker and Roth (2000) and Brand et al. (1994). Pitfall traps are commonly used for the collection of surface active animals, like spiders and beetles. The high number of species recorded, the continuous nature of the sampling, the easy and cheap handling and low maintenance favour the use of pitfall traps, despite some limitations (for discussion see Luff 1975; Uetz and Unzicker 1976; Curtis 1980; Phillips and Cobb 2005). Emergence traps (Bodenphotoeklektor Modell 250, ecotech GmbH, Bonn, Germany) were cone shaped tents without a bottom. The frame of the tent (ground surface 0.25 m²) is worn in the humus layer, a pitfall trap is on the bottom, and on top of the tent a box is fixed containing coppersulphate (1%). The traps were established in each stand by placing them randomly close to the centre of each plot (ca. 10 m apart from each other), and close to other investigations made on the plots (for example elemental concentrations in seepage water, emission of trace gases, and meteorological measurements). At the small-scale clear-cut the distance between traps on CCB and on CCS and the distance to the nearest uncut stand was ca. 25 m. The trapping period covered most of the growing season (May–October) as recommended by Riecken (1999). The animals were collected three times a year (spring, summer, and autumn). The traps were emptied 2 weeks after positioning. All captured animals were transferred into 70% isopropanol and assigned to taxonomic

groups. Pitfall traps were plastic jars (diameter 75 mm, depth 100 mm) partly filled with ethyleneglycol. A transparent plastic roof (18 cm×18 cm) was placed ca. 15 cm above the trap to prevent flooding from rainwater. Spider species were identified from the pitfall and emergence traps by a specialised expert (Helmut Stumpf, Würzburg, Germany), who also deposited the voucher specimens in his private collection. When species descriptions are based only on the genitalia, only sexually mature spiders were identified to species. Juvenile and penultimate stages were then only identified according to their genus or family. Some damaged individuals were unidentifiable. Besides spiders, numbers of individuals of other groups/families of animals were also counted. Collembola (separated into the groups Symphyleona and Entomobryomorpha), Carabidae (forest species and open habitat species according to Huber and Baumgarten 2005), Staphylinidae, Curculionidae, Elateridae, Isopoda, Gastropoda, Opiliones, Heteroptera and Myriapoda were used as environmental variables in the multivariate analyses (see Huber and Baumgarten 2005). The coverage of different species of ground vegetation close to the pitfall traps (2.0 m) was estimated for all years.

Photoactive radiation (PAR) was measured at 1 m height with a Licqor Par sensor. The measurements were used in detrended correspondence analysis (DCA; Hill and Gauch 1980 with corrections of Oksanen and Minchin, 1997), using the PC-ORD4 software package for windows (McCune et al. 2002). We first studied whether clear-cutting or felling-cutting affect the yearly catches of spider families in pitfall traps. We excluded from the analysis spider families with two or fewer individuals per plot and year. After these modifications we included in the analysis 19 environmental variables and 12 spider families. Second, we studied the effects of the treatments on total catches (pitfall + emergence traps) of the 20 dominant species. Referring to literature (Heydemann 1964; Jones 1990; Heimer and Nentweg 1991; Platen et al. 1991; Blick and Scheidler 2003) we made distinctions about size classes, ecology, and preferred habitat. Statistical analyses were performed with SPSS 11.5.1, SPSS Inc to study the effects of the treatments on the parameters size class, web, habitat, humidity preferences, stratum preference and stratum preference of ground dwellers for each year. Because all parameters were non-Gaussian distributed (Kolmogorov–Smirnov goodness of fit tests) and not equal in variance (Levene statistics), data were analysed using the non-parametric Kruskal–Wallis test. If significant differences among the treatments occurred, a multiple comparison was carried out with the non-parametric Mann–Whitney-*U*-test. The significance level used throughout was 5%.

Results

In total we sampled 7101 individuals (4468 adults and 2633 juveniles), of which 4530 individuals could be identified (Figure 1 and Appendix Table A1). The

number of individuals were highest in the pre-treatment year 1999 (Figure 1), while in the following years the number of individuals decreased. This was mostly due to the significantly higher number of individuals in 1999 during the first (May–June), and third (October) sampling period, while the numbers of individuals during the summer periods was not significantly different. The numbers of identified individuals were significantly lower at both clear-cut plots (CCB, CCS) in 2000 and 2001. In total 107 species of 16 families were identified with 70 species (35–44 species yearly) on the mature spruce plots (control plot, or plots before cutting, Figure 1) within 3 years of investigation. On the two clear-cut treatments 78 species were found after the cutting, with 63 species in 2000 (48 on CCB, 42 on CCS), and 45 species in 2001 (29 each on CCB and CCS). Fifteen species from seven families comprised more than 1% of the sample (printed in bold in Appendix Table A1). *Coelotes terrestris* was the dominant species with 1332 individuals followed by *Tapinocyba pallens* (615). Forty species appeared in all of the three investigation years with *Walckenaeria atrotibialis* the only species found every year on each plot. Linyphiidae and Amaurobiidae numerically dominated the control (Table 1). The first step in femel-cutting did not change the dominance of these two families. Individuals of the family Lycosidae, of which very few were collected before the clear-cut, dominated the clear-cut stand regenerated with beech in both years after the cutting. The clear-cut stand regenerated with spruce showed a delayed response compared to the beech regeneration plot, with Lycosidae dominating in the year after cutting (2001), but not in the year of cutting (2000).

Xerolycosa nemoralis was the only species that could be found exclusively on the clear-cuts, but not on the control or on the femel-cut. Only the Lycosidae *Pardosa lugubris*, *Trochosa terricola*, *Xerolycosa nemoralis*, and the Gnaphosidae *Zelotes cliviculus* were found in both clear-cut treatments after the cutting with two or more individuals. The most frequent spider species of the control were not collected after clear-cutting or decreased to very low values. The four most common species of the control, *Coelotes terrestris*, *Tapinocyba pallens*, *Coelotes inermis*, and *Agyrta ramosa* (all Linyphiidae or Amaurobiidae), were not collected in the year after clear-cutting on one of the clear-cuts and presented with only a few individuals at the other clearcut. *Tenuiphantes tenebricola* and *Gongylidiellum latebricola*, both Linyphiidae, were not collected in the year after the clear-cut. The number of individuals of Linyphiidae decreased after clear-cutting, but the family was still the second largest in number of individuals on the clear-cut plots until the end of the investigation.

Table 2 describes the changes of functional groups before and after cutting (see Appendix Table A1 for classification). The size distribution of spiders changed after clear-cutting. The number of individuals from the smallest size class 1 (0–3 mm) and the biggest size class 4 (>10.5 mm) decreased, whereas the number of individuals in size class 3.0–10.5 mm increased (Table 2). The number of individuals of web building spiders dramatically decreased after the clear-cut. Funnel web spiders (Agelenidae) were totally absent on the clear-cut in the year after the cutting. Also very few hackledmesh weavers (Amaurobiidae)

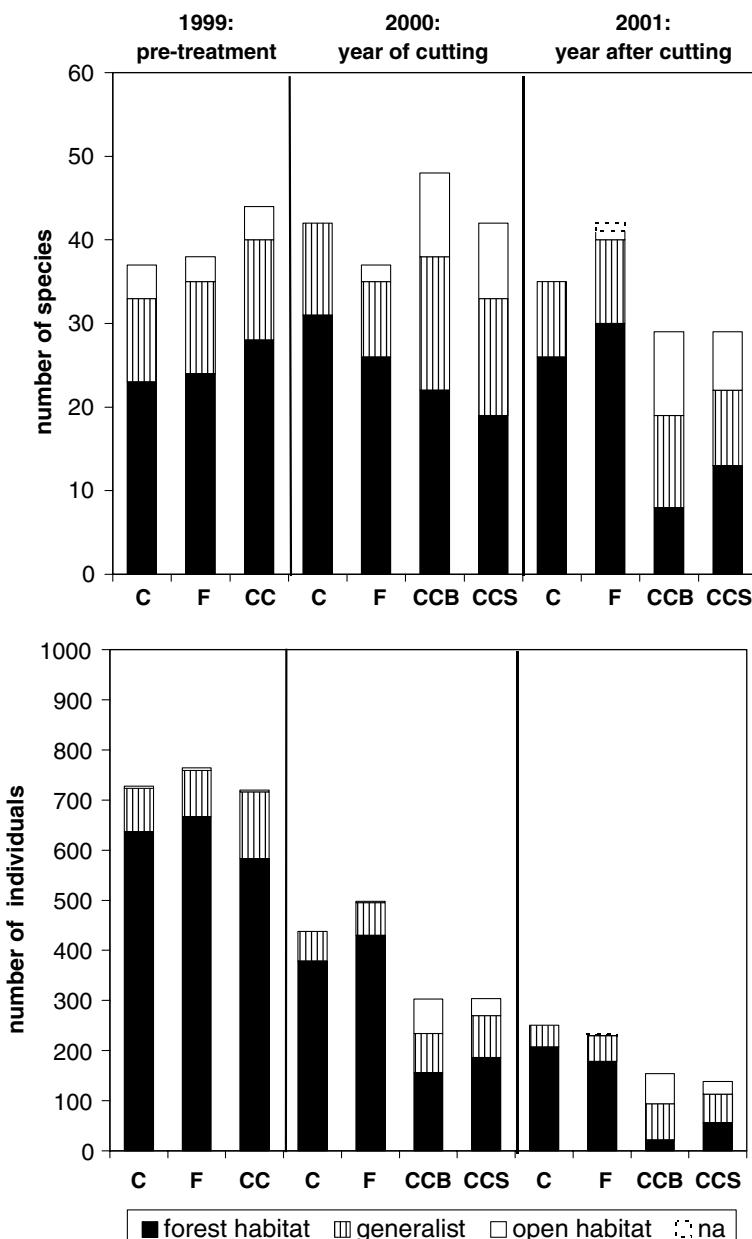


Figure 1. Total number, number of forest habitat, generalists, and open habitat spider species (above), and identified individuals (below), in 1999 (pre-treatment year), 2000 (year of cutting), and 2001 (year after the cutting) for each treatment. C = control, F = female, CC = clear-cut, CCB = clear-cut beech, CCS = clear-cut spruce.

Table 1. Percentage of number of individuals of spider families for each treatment in the sampling years 1999 (pre-treatment year), 2000 (year of cutting) and 2001 (year after cutting).

| Family | 1999 | | | 2000 | | | | 2001 | | | |
|----------------|------|----|----|------|----|-----|-----|------|----|-----|-----|
| | C | F | CC | C | F | CCB | CCS | C | F | CCB | CCS |
| Agelenidae | 2 | 1 | 1 | 2 | 2 | 0 | 0 | 2 | 3 | 0 | 0 |
| Amaurobiidae | 41 | 47 | 39 | 48 | 48 | 10 | 36 | 40 | 31 | 4 | 14 |
| Araneidae | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 |
| Clubionidae | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 5 | 2 | 0 | 1 |
| Dictynidae | 2 | 2 | 3 | 0 | 1 | 0 | 1 | 4 | 5 | 1 | 2 |
| Dysderidae | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Gnaphosidae | 0 | 0 | 0 | 0 | 0 | 2 | 3 | 0 | 0 | 3 | 11 |
| Hahniidae | 0 | 1 | 4 | 0 | 0 | 1 | 5 | 0 | 2 | 0 | 9 |
| Linyphiidae | 50 | 46 | 45 | 42 | 46 | 19 | 39 | 40 | 48 | 13 | 20 |
| Lycosidae | 0 | 0 | 3 | 2 | 0 | 66 | 9 | 1 | 2 | 64 | 37 |
| Philodromiidae | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 |
| Salticidae | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 2 | 1 |
| Segestriidae | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 0 |
| Tetragnatidae | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 2 | 1 |
| Theridiidae | 1 | 1 | 1 | 2 | 0 | 1 | 2 | 2 | 1 | 1 | 2 |
| Thomisidae | 1 | 1 | 2 | 1 | 2 | 0 | 2 | 2 | 3 | 9 | 2 |

Treatment: C = control, F = femel, CC = clear-cut, CCB = clear-cut beech, CCS = clear-cut spruce.

were collected on the clear-cut plots (Table 1). Nearly all Amaurobiidae collected on the clear-cuts were juvenile, while adult species were absent.

Within the year after clear-cutting a significant increase took place in the total number of open habitat species, mostly free hunting spiders like Lycosidae and Thomisidae (Table 1). The number of individuals of forest species decreased significantly after clear-cutting from the year of cutting to the year after cutting. There was no significant effect in this parameter by femel-cutting. After clear-cutting the number of individuals that are hygrophilic or favour medium moisture conditions decreased, while increases were exhibited in the number of individuals favouring dry conditions (xerophilous), or that are independent (euryoecious) in relation to moisture. On the control plot hygrophilic individuals were much lower in the years 2000 and 2001 compared with 1999, while the number of individuals with middle moisture preferences was much lower in 2001 than in previous years.

The number of individuals living preferentially below the ground decreased drastically after clear-cutting. The fraction of individuals preferring an uncovered habitat on the ground or grass mulch increased, while individuals preferring a humus layer with mosses decreased.

Figure 2 describes the results of DCA analysis of the total catches (pitfall traps + emergence traps) of the 20 most numerous spider species in the different years and treatments. The mature spruce plots (CCB, and CCS in the pre-treatment year, and plot C in all three years) together with the femel-cut

Table 2. Average number of identified individuals per trap (emergence + pitfall traps) with standard error attributed to the parameters: habitat fixation, size class, web, humidity preference, stratum preference, and stratum preference of ground dwellers according to the data in Appendix Table A1.

| Parameter | 1999 | | | | | | 2000 | | | | | | 2001 | | | | | |
|---------------------------------------|-----------------|---------------|---------------|---------------|--------------|--------------|--------------|--------------|--------------|--------------|-------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|
| | C | F | CC | C | F | CCB | CCS | C | F | CCB | CCS | C | F | CCB | CCS | C | F | CCB |
| Total | 45.5 ± 3.5 a | 47.8 ± 3.6 a | 45.0 ± 3.8 a | 27.4 ± 4.2 ab | 31.1 ± 3.6 a | 20.2 ± 1.7 b | 19.0 ± 1.5 b | 15.7 ± 2.1 a | 14.5 ± 1.5 a | 9.6 ± 1.1 b | 9.2 ± 1.4 b | 14.5 ± 1.5 a |
| Size class | <3 mm | 25.4 ± 2.8 a | 23.8 ± 4.5 a | 24.9 ± 3.0 a | 11.6 ± 1.7 a | 12.7 ± 1.0 a | 9.2 ± 1.3 a | 10.1 ± 1.4 a | 8.2 ± 1.2 a | 7.4 ± 1.3 a | 2.7 ± 0.4 b | 3.9 ± 0.9 b | 2.7 ± 1.2 a |
| | >3–10.5 mm | 3.1 ± 0.4 a | 1.8 ± 0.4 b | 4.4 ± 0.6 a | 2.1 ± 0.5 c | 2.3 ± 0.3 c | 8.9 ± 1.0 a | 4.8 ± 0.7 b | 2.9 ± 0.4 c | 3.3 ± 0.6 bc | 6.9 ± 0.9 a | 4.7 ± 0.8 ab | 3.3 ± 0.6 bc |
| | >10.5 mm | 18.9 ± 4.1 a | 22.1 ± 4.1 a | 15.6 ± 3.1 a | 13.6 ± 3.1 a | 16.2 ± 3.2 a | 2.1 ± 0.5 c | 4.0 ± 0.7 b | 4.6 ± 1.3 a | 3.6 ± 0.9 a | 0.6 ± 0.3 b | 0.6 ± 0.3 b | 4.6 ± 1.3 a |
| Web | No web | 1.1 ± 0.3 b | 0.9 ± 0.3 b | 3.1 ± 0.5 a | 0.8 ± 0.3 c | 0.4 ± 0.2 c | 8.4 ± 0.9 a | 4.2 ± 0.7 b | 0.9 ± 0.2 c | 1.0 ± 0.3 c | 6.9 ± 0.7 a | 4.6 ± 0.7 b | 1.0 ± 0.3 c | 6.9 ± 0.7 a | 1.0 ± 0.3 c | 6.9 ± 0.7 a | 1.0 ± 0.3 c | 6.9 ± 0.7 a |
| | Web | 44.4 ± 3.5 a | 46.8 ± 3.6 a | 41.9 ± 3.5 a | 26.6 ± 4.2 a | 30.8 ± 3.5 a | 11.8 ± 1.4 b | 14.8 ± 1.3 b | 14.8 ± 2.1 a | 13.5 ± 1.6 a | 2.7 ± 0.5 b | 4.6 ± 1.0 b | 13.5 ± 1.6 a | 2.7 ± 0.5 b | 13.5 ± 1.6 a | 2.7 ± 0.5 b | 13.5 ± 1.6 a | 2.7 ± 0.5 b |
| Habitat fixation | Open habitats | 0.3 ± 0.2 a | 0.2 ± 0.1 a | 0.3 ± 0.1 a | 0.0 ± 0.0 c | 0.1 ± 0.1 c | 5.0 ± 0.6 a | 2.3 ± 0.5 b | 0.0 ± 0.0 c | 0.0 ± 0.0 c | 3.9 ± 0.6 a | 1.9 ± 0.4 b | 0.0 ± 0.0 c | 3.9 ± 0.6 a | 0.0 ± 0.0 c | 3.9 ± 0.6 a | 0.0 ± 0.0 c | 3.9 ± 0.6 a |
| | Generalist | 5.3 ± 0.5 a | 5.6 ± 1.2 a | 8.3 ± 2.1 a | 3.8 ± 0.6 a | 4.1 ± 1.0 a | 4.9 ± 0.6 a | 5.2 ± 0.7 a | 2.8 ± 0.4 a | 3.3 ± 0.5 a | 4.4 ± 0.7 a | 3.5 ± 0.9 a | 3.3 ± 0.5 a | 4.4 ± 0.7 a | 3.3 ± 0.5 a | 4.4 ± 0.7 a | 3.3 ± 0.5 a | 4.4 ± 0.7 a |
| | Forest habitats | 39.9 ± 3.2 a | 42.0 ± 3.5 a | 36.5 ± 2.6 a | 23.6 ± 3.9 a | 26.9 ± 3.7 a | 10.3 ± 1.4 b | 11.6 ± 1.1 b | 12.9 ± 1.9 a | 11.2 ± 1.4 a | 1.4 ± 0.4 b | 3.7 ± 1.0 b | 11.2 ± 1.4 a | 1.4 ± 0.4 b | 11.2 ± 1.4 a | 1.4 ± 0.4 b | 11.2 ± 1.4 a | 1.4 ± 0.4 b |
| Humidity preference | Hygrophil | 23.0 ± 2.0 a | 23.4 ± 2.9 a | 23.8 ± 2.6 a | 8.0 ± 1.3 a | 9.1 ± 1.2 a | 6.9 ± 1.0 a | 7.8 ± 1.1 a | 7.2 ± 1.2 a | 6.5 ± 0.8 a | 2.1 ± 0.3 b | 2.8 ± 0.7 b | 6.5 ± 0.8 a | 2.1 ± 0.3 b | 6.5 ± 0.8 a | 2.1 ± 0.3 b | 6.5 ± 0.8 a | 2.1 ± 0.3 b |
| | Mid humid/dry | 18.7 ± 3.2 ab | 21.8 ± 2.7 a | 13.3 ± 2.0 b | 15.5 ± 3.2 a | 18.8 ± 2.7 a | 3.0 ± 0.7 c | 4.8 ± 0.6 b | 4.9 ± 0.8 a | 4.9 ± 0.8 a | 0.2 ± 0.1 b | 0.6 ± 0.2 b | 0.2 ± 0.1 b |
| | Euryoecious | 0.3 ± 0.2 a | 0.2 ± 0.1 a | 0.3 ± 0.2 a | 0.2 ± 0.1 c | 0.1 ± 0.1 c | 4.0 ± 0.5 a | 1.5 ± 0.4 b | 0.7 ± 0.2 b | 0.6 ± 0.2 b | 2.3 ± 0.4 a | 0.7 ± 0.3 b | 0.6 ± 0.2 b | 2.3 ± 0.4 a | 0.6 ± 0.2 b | 2.3 ± 0.4 a | 0.6 ± 0.2 b | 2.3 ± 0.4 a |
| | Xerophil | 3.5 ± 0.7 b | 2.4 ± 0.6 b | 7.6 ± 0.8 a | 3.8 ± 0.7 ab | 3.2 ± 0.7 b | 5.9 ± 0.9 a | 4.9 ± 0.6 a | 2.9 ± 0.5 b | 2.4 ± 0.4 b | 5.2 ± 0.7 a | 4.8 ± 0.8 a | 2.9 ± 0.5 b | 2.4 ± 0.4 b | 5.2 ± 0.7 a | 2.4 ± 0.4 b | 5.2 ± 0.7 a | 2.4 ± 0.4 b |
| Stratum preference | Underground | 10.0 ± 2.1 a | 11.4 ± 2.1 a | 8.1 ± 1.6 a | 7.2 ± 1.6 a | 8.5 ± 1.7 a | 1.2 ± 0.3 b | 2.0 ± 0.3 b | 2.7 ± 0.7 a | 2.2 ± 0.5 a | 0.0 ± 0.0 c | 0.3 ± 0.1 b | 2.2 ± 0.5 a | 0.0 ± 0.0 c | 0.3 ± 0.1 b | 0.0 ± 0.0 c | 0.3 ± 0.1 b | 0.0 ± 0.0 c |
| | Ground-dwelling | 31.8 ± 2.1 a | 32.5 ± 3.0 a | 30.2 ± 2.7 a | 16.8 ± 2.4 a | 19.6 ± 2.0 a | 16.6 ± 1.5 a | 14.4 ± 1.5 a | 8.9 ± 1.0 a | 8.6 ± 0.8 a | 7.5 ± 0.9 a | 7.4 ± 1.3 a | 8.9 ± 1.0 a | 7.5 ± 0.9 a |
| | Above-ground | 3.4 ± 0.5 b | 3.8 ± 0.8 b | 6.7 ± 0.8 a | 2.9 ± 0.6 a | 3.0 ± 0.4 a | 2.4 ± 0.6 a | 2.6 ± 0.5 a | 4.1 ± 0.8 a | 3.6 ± 0.9 a | 2.1 ± 0.3 b | 1.5 ± 0.4 b | 3.6 ± 0.9 a | 2.1 ± 0.3 b | 1.5 ± 0.4 b | 2.1 ± 0.3 b | 1.5 ± 0.4 b | 2.1 ± 0.3 b |
| Stratum preference of ground dwellers | Uncovered | 0.0 ± 0.0 a | 0.0 ± 0.0 a | 0.0 ± 0.0 a | 0.0 ± 0.0 b | 0.0 ± 0.0 b | 0.3 ± 0.1 a | 0.2 ± 0.1 a | 0.0 ± 0.0 b | 0.0 ± 0.0 b | 0.8 ± 0.3 a | 0.3 ± 0.2 a | 0.0 ± 0.0 b | 0.8 ± 0.3 a | 0.3 ± 0.2 a | 0.0 ± 0.0 b | 0.8 ± 0.3 a | 0.3 ± 0.2 a |
| | Moss | 12.3 ± 1.0 a | 10.5 ± 1.5 ab | 9.2 ± 0.9 b | 5.1 ± 0.9 a | 5.5 ± 0.7 a | 2.3 ± 0.3 b | 2.9 ± 0.3 b | 2.3 ± 0.3 a | 1.8 ± 0.2 a | 0.6 ± 0.2 b | 0.9 ± 0.5 b | 2.3 ± 0.3 a | 1.8 ± 0.2 a | 0.6 ± 0.2 b | 0.9 ± 0.5 b | 2.3 ± 0.3 a | 1.8 ± 0.2 a |
| | Litter | 16.5 ± 1.3 a | 18.5 ± 1.4 a | 16.9 ± 1.4 a | 9.3 ± 1.3 a | 11.1 ± 1.4 a | 6.8 ± 0.9 b | 7.1 ± 0.9 ab | 4.9 ± 0.7 ab | 5.0 ± 0.6 a | 3.3 ± 0.4 b | 4.0 ± 0.8 ab | 5.0 ± 0.6 a | 3.3 ± 0.4 b | 4.0 ± 0.8 ab | 5.0 ± 0.6 a | 3.3 ± 0.4 b | 4.0 ± 0.8 ab |
| | Grass | 2.5 ± 0.2 a | 3.1 ± 0.6 a | 3.8 ± 0.7 a | 2.1 ± 0.3 c | 2.6 ± 0.4 bc | 6.5 ± 0.7 a | 3.3 ± 0.5 b | 1.2 ± 0.2 b | 1.6 ± 0.2 b | 2.7 ± 0.4 a | 1.7 ± 0.4 ab | 1.6 ± 0.2 b | 2.7 ± 0.4 a | 1.7 ± 0.4 ab | 1.6 ± 0.2 b | 2.7 ± 0.4 a | 1.7 ± 0.4 ab |

Sampling years: pre-treatment year (1999), year of cutting (2000), and year after the cutting (2001). Treatments: C = control, F = fenned, CC = clear-cut, CCB = clear-cut beech, CCS = clear-cut spruce. Different letters indicate a statistically significant ($p < 0.05$) difference between the treatments for each investigated year.

plot (F) are clearly separated from the clear-cut plots CCB and CCS after the felling. Factors reflecting clear-cut conditions (higher radiation, precipitation, and number of individuals of open habitat Carabidae) were on the optimum right of the origin. Factors reflecting dense forest conditions (for example: coverage of mosses, forest species of Carabidae, Curculionidae, Staphylinidae) were on the optimum left of the origin. One ‘forest and open habitat’ species (the Linyphiidae *Gongylidiellum latebricola*), and six forest species (the Linyphiidae *Tenuiphantes tenebricola*, *Tapinocyba pallens* and *Walckenaeria alticeps*, the Agelenidae *Histopona torpida*, and the Amaurobiidae *Coelotes terrestris* and *Coelotes inermis*) are clustered left of the origin of the ordination together with the untreated or femel stands. The number of individuals of these species drastically decreased (or were totally absent) on the clear-cut in the year of cutting (2000) and after the cutting (2001). ‘Open habitat’ or ‘forest and open habitat’ (generalist) species were clustered on the right side of the ordination, together with the clear-cut plots. The Lycosidae *Xerolycosa nemoralis*,

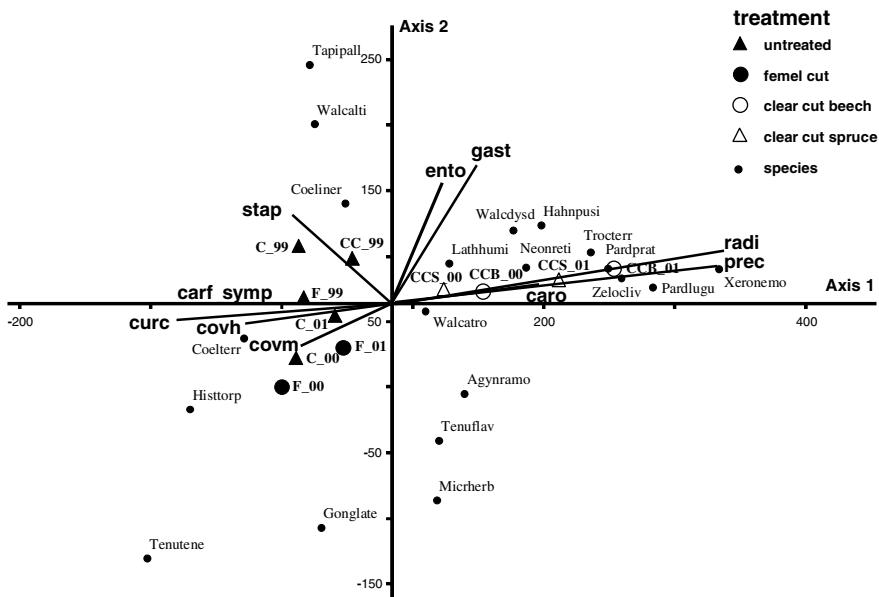


Figure 2. DCA ordination of the 20 most numerous species in the different treatments for the total catch of pitfall and emergence traps. _99 = year 1999 (pre-treatment year), _00 = year 2000 (year of cutting), _01 = year 2001 (year after cutting). Treatments: C = control, F = femel, CCB = clear-cut beech, CCS = clear-cut spruce. All plots within the pre-treatment year and the control plot are marked as ‘Untreated’. The eight-letter abbreviations indicate the species, e.g. Coelterr = *Coelotes terrestris*. Abbreviations of the species are listed in Appendix Table A1. Lable explanations: gast = number of individuals of Gastropoda, ento = Entomobryomorpha, symp = Symphypleona, curc = Curculionidae, stap = Staphylinidae, carf = Carabidae of forest habitats, caro = Carabidae of open habitats, prec = precipitation, radi = photosynthetic active radiation, covh = coverage of herbs, covm = coverage of mosses.

Pardosa lugubris, *Pardosa prativaga*, *Trochosa terricola* and the Gnaphosidae *Zelotes cliviculus* were nearly absent in the spruce stand before, but were favoured by clear-cutting. The species *Neon reticulatus*, *Hahnia pusilla*, *Walckenaeria dysderoides* and *Lathys humilis* showed (1) no clear effect of treatment, (2) strong year-to-year fluctuations, or (3) pre-treatment differences. Three species (all Linyphiidae), *Walckenaeria atrotibialis*, *Agynta ramosa*, *Micrargus herbigradus*, right of the origin and below axis 1 showed a delayed response of the clear-cut treatment with a clear effect only in 2001.

The multivariate analyses from all pitfall traps with the spider families showed the following results (Figure 3a, b). Nearly all pitfall traps from the femele-cutting and the control plot were clustered left of the centre. Traps from the clear-cut plots are separated from these traps. Traps from the CCS plot showed a delayed response, indicating that most of the traps were close to the control traps in the year of cutting, but were clearly separated in the year after the cutting. The families Amaurobiidae, Clubionidae, Agelenidae, and Linyphiidae were clustered on the left side of the centre. The Lycosidae were close to the vectors precipitation and radiation, which indicate clear-cut conditions.

Discussion

The number of individuals in the control decreased from 1999 to 2001. The reasons for this decrease are unclear. One can assume that this decrease may be the effect of repeating sampling. However, summer sampling data were very similar for all years. Also, climatic factors may be responsible for the difference between years. For example, in the year 2000 the decrease was restricted to individuals with a hygrophilic humidity preference (see Table 2). This finding is in good agreement with a very dry period during the first sampling period in June 2000, while 1999 was characterised with heavy rainfall during this period. September 1999 was the warmest September of the century, but with enough rain. These climate conditions may be responsible for the high number of individuals sampled in autumn 1999. The year 2001 was characterised by a soil frost at the beginning of the year, which is very unusual on this site and a long winter period until April. The first sampling period was first very dry and hot, followed by heavy rain. This climatic situation may be reflected in the lower number of individuals (1) with stratum preference ‘underground’, and (2) hygrophilic to mid humid/dry humidity preferences (see Table 2).

The number of species of the investigated even-aged spruce stand at the Högwald is in the range of more natural beech forests in Southern Germany (Dumpert and Platen 1985; Brand et al. 1994). The dominant families at our site were Linyphiidae and Amaurobiidae. This was also reported in other investigations of deciduous and coniferous stands in southern Germany (Brand et al. 1994; Engel 1999; Junker et al. 2000). Linyphiidae also dominated in Scots and Lodgepole pine stands in Scotland (Docherty et al. 1997), in coniferous stands in southern Finland (Pajunen et al. 1995), with Agelenidae

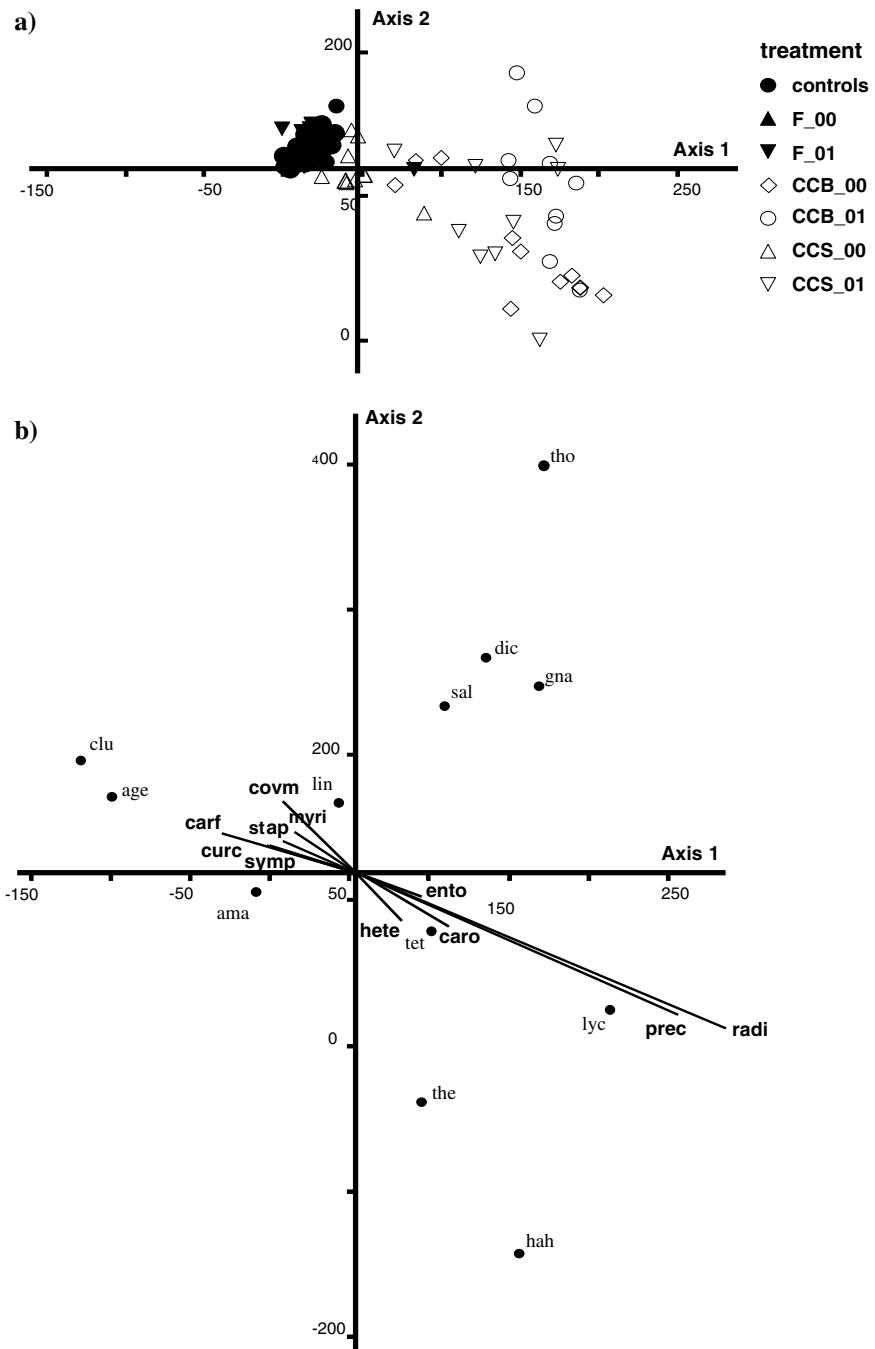




Figure 3. (a) DCA ordination for single pitfall traps for the years 1999 (pre-treatment), 2000 (year of cutting) and 2001 (year after cutting). (b) DCA ordination of the twelve most numerous families sampled during 1999–2001. The three-letter abbreviations indicate the families, e.g. Lin = Linyphiidae. Abbreviations of the spider families are listed in Appendix Table A1. ‘Controls’ are all pitfall traps from the pre-treatment year and of the control in 2000 and 2001. _00 = year 2000, _01 = year 2001. F = femel, CCB = clear-cut beech, CCS = clear-cut spruce. Table explanations: ento = number of individuals of Entomobryomorpha, symp = Symphypleona, curc = Curculionidae, stap = Staphylinidae, hete = Heteroptera, caro = Carabidae of open habitats, carf = Carabidae of forest habitats, myri = Myriapoda, prec = amount of precipitation, radi = yearly photosynthetic active radiation, covm = coverage of mosses.

in an ‘old growth’ coniferous forest in Oregon, USA. (McIver et al. 1992), and with Amaurobiidae and Agelenidae in a dense spruce fir forest of Maine, USA (Jennings et al. 1988). Lycosidae were absent or scarce in our spruce stand and in other mature forests (Bultman et al. 1982; Jennings et al. 1988; Brand et al. 1994). In contrast to these results, Lycosidae were the dominant family in a study of mature boreal forests (aspen, mixed wood, and spruce) in Canada (Pearce et al. 2004). However, in this study the stands had open canopies with an average tree cover of only 12–20%.

Spider assemblages responded quickly within the year of clear-cutting in our experiment as in the investigation of Buddle et al. (2000) after wildfire and clear-cutting. While the total number of species was more or less unaffected, the number of forest habitat species decreased, and the number of open habitat species increased. After clear-cutting, free hunting spiders (mostly Lycosidae) were favoured in our study. This guild is more mobile than web builders and therefore has a greater flexibility (Pearce et al. 2004). The increase of Lycosidae and the decrease of Linyphiidae in our study following clear-cutting have also been reported by other studies in different regions of the world (Huhta 1971; Coyle 1981; Curry et al. 1985; Jennings et al. 1988; McIver et al. 1992; Pajunen et al. 1995; Atlegrim and Sjöberg 1995; Pearce et al. 2004).

After the clear-cutting, we observed a distinct increase of Gnaphosidae (mainly *Zelotes clivicoles*). This was also the case after clear-cutting in coniferous forests of Finland (Pajunen et al. 1995). The Gnaphosidae prefer nearly exclusively the clear-cut habitat in our study, as in the study of Buddle et al. (2000), where *Gnaphosa borea* was exclusively discovered in fire-originated stands.

After clear-cutting a dramatic decrease in the number of spiders with habitat preferences ‘below the ground’ (for example in the humus layer) or of species preferring the moss layer took place (see also Siira-Pietikäinen et al. 2003). Spiders react preferentially to abiotic factors like humidity, temperature, and light (Huhta 1971; Platen et al. 1991). Tree species, mixtures of tree species, dead wood or microhabitat attributes seem to be of lower importance (Platen et al. 1991; Engel 1999; Pearce et al. 2004) compared to tree cutting procedures. Therefore one can assume that the decrease of ‘underground species’ on the clear-cuts can be explained with an increase in maximum and average temperature in the uppermost sub-layers of the humus layer during summer.

Furthermore, these layers were periodically drier at the clear-cut than at the control. After clear-cutting, the humus layer became thinner due to an increase in mineralisation and a decrease in litter fluxes due to the absence of the mature stand. Only free hunting spiders like the Lycosidae were favoured under such conditions because they are typical field inhabitants, best suited for locomotion in habitats where little litter accumulates, or where litter has been removed (Uetz 1979; Bultman et al. 1982). The decrease of spiders with moss habitat preferences corresponds well with the decrease in coverage of mosses after clear-cutting as a result of a higher light intensity.

Our results of the DCA analysis indicate that Agelenidae and Amaurobiidae prefer the very dense parts of the spruce forest at the Höglwald site, which have not been thinned for some decades. After clear-cutting the Amaurobiidae decreased dramatically in our experiment, as well as after a wind throw of a beech forest in southern Germany (Brand et al. 1994). Linyphiidae also preferred the forest interior, but some species were also numerous in the clear-cuts. Linyphiidae inhabit complex microhabitats in the leaf litter and soil of forests (Huhta 1971; Buddle et al. 2000), but they are also believed to survive harvesting by moving deep into the litter (Buddle et al. 2000). Besides a low heat tolerance, the decrease in ground cover of shrubs following clear-cutting should decrease the opportunity to spin webs and lower the habitat quality for this spider group (Huhta 1971; Atlegrim and Sjöberg 1995). However, at the mature spruce stand at the Höglwald site nearly no shrubs were present before the cutting. On the contrary, a new structure was established with planting of the spruce and beech saplings. In our felling-cutting treatment the spider fauna did not significantly differ from that in the untreated spruce stand (Atlegrim and Sjöberg 1995) despite the fact that some new structures were generated after the felling (beech sapling layer, tree stumps, branches left on the site, etc.).

Clear-cut habitats are more heterogeneous in two dimensions (Huber and Baumgarten 2005; Pearce et al. 2004) with water filled ruts, uncovered microhabitats, different vegetation structures and so on. Nevertheless, the number of species on the clear-cut plots was not higher in the year after cutting (2001) than in the pre-treatment period, or on the control or felling-cut. Coyle (1981), Atlegrim and Sjöberg (1995), and Buddle et al. (2000) also found fewer numbers of individuals after clear-cutting, while more individuals of spiders were collected after a wind throw in Germany (Brand et al. 1994) or in clear-cuts in Canada (Pearce et al. 2004) compared to the control.

Collembola are regarded as the most important prey of small spiders, owing to their abundance, appropriate size (0.2–5 mm), thin integument and relative defencelessness (Huhta 1971). The number of Collembola (mainly Entomobryomorpha) increased enormously after clear-cutting at the Höglwald site (data not shown) or in other experiments (Huhta et al. 1967, 1969). However, the total number of adult spiders did not show this same trend. Huhta et al. (1967) also observed no increase in the spider populations after a fertiliser-induced increase of Collembola. The number of potential prey animals seems not to influence the size of spider populations (Kajak 1965; Turnbull 1966; Huhta 1971).

Forest spiders may recover relatively rapidly after disturbances, when there is a possibility to rebuild the communities from uncut stands. Huhta (1971) found that forest spider assemblages began resembling those of an old pine/spruce forest between 7 and 13 years after burning and clear-cutting. After around 15 years of forest growth web building forest species became increasingly dominant (Buddle et al. 2000), with succession of the forest toward canopy closure (Huhta 1971) and a recovery of the spider assemblages was apparent 30 years after clear-cutting (McIver et al. 1992).

Conclusions

The untreated homogenous Norway spruce stands at the Höglwald site exhibited a relatively high diversity of spider species. The spider community exhibited a fast and pronounced change in species composition after clear-cutting, which is clearly reflected in the ecological demands of the newly occurring species on the clear-cut. If the forest spider species of mature stands should be preserved during the regeneration process in the hope that this group best fulfils the functionality of the system, femel-cutting should be favoured. The final cutting in this long lasting process should be done after a dense regeneration has been established. This procedure will also help to reduce the risk of nitrate leaching (see Huber et al. 2004b). A dense natural or planted regeneration before clear-cutting may also help to preserve the original community due to the shading effect, or at least help to slow down the effects of clear-cutting on forest species. Indications from literature are given that even in clear-cuts a typical forest species community of spiders will be re-established after approx. 30 years. As a requirement, enough areas of dense mature stands in the forest should be left as retreats for the forest species. Long-term investigations are needed to give more information about species composition after femel- and clear-cutting, also taking into account periods of a possible return of forest species in later years. However, such investigations are still rare in ecological research due to the pattern of funding for research (Tilman, 1989). Further, investigations on various sites are needed, which compare the regeneration methods in the region to give more insight about the heterogeneity/diversity of spiders on a landscape scale.

Acknowledgements

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Appendix A.

Table A1. Number of individuals of identified species and corresponding ecological parameters size class (SC), web, habitat (HAB), moisture demand (MD), and stratum (STR) for each treatment in 1999 (pre-treatment year), 2000 (year of cutting), and 2001 (year after cutting).

| Family | Species | Abbr. | 1999 | | | 2000 | | | 2001 | | | Σ | | | SC | Web | HAB | MD | STR |
|-----------------------|--------------------------------------------------|------------------|------|-----|-----|------|-----|-----|------|----|----|----------|-----|------|----|-----|-----|-----|---------|
| | | | C | F | CC | C | F | CCB | CCS | C | F | CCB | CCS | C | F | CCB | CCS | | |
| Agelenidae (Age) | <i>Histopona torpida</i> (C.L. KOCH, 1834) | <i>Historp</i> | 16 | 9 | 8 | 13 | 11 | 1 | 0 | 9 | 10 | 0 | 0 | 77 | 3 | 1 | F | h | 0-11 |
| Amaurobiidae (Ama) | <i>Amaurobius fenerstralis</i> (STROEM, 1768) | | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 7 | 8 | 0 | 0 | 17 | 3 | 1 | F | eu | 0-2 |
| | <i>Amaurobius ferox</i> (WALCKENAER, 1830) | | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 4 | 1 | O | x | 0-1g |
| | <i>Amaurobius</i> sp. | | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | - | - | - | - | - |
| | <i>Coelotes inermis</i> (L. KOCH, 1855) | <i>Coeliner</i> | 49 | 63 | 76 | 13 | 16 | 7 | 9 | 25 | 21 | 0 | 5 | 284 | 4 | 1 | F | h | 0-11 |
| | <i>Coelotes</i> sp. | | 54 | 95 | 99 | 79 | 91 | 74 | 148 | 67 | 33 | 12 | 25 | 777 | - | - | - | - | - |
| | <i>Coelotes terrenus</i> (WIDER, 1834) | <i>Coeltterr</i> | 251 | 291 | 174 | 204 | 243 | 25 | 55 | 48 | 37 | 0 | 4 | 1332 | 4 | 1 | F | mid | 0-11, m |
| Araeidae (Ara) | Araneidae sp. | | 0 | 0 | 0 | 1 | 1 | 0 | 6 | 1 | 0 | 0 | 0 | 9 | - | - | - | - | - |
| | <i>Aramaeus angulatus</i> (CLERCK, 1757) | | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 4 | 1 | F | h | 2 |
| | <i>Aramaeus sturmi</i> (HAHN, 1831) | | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 1 | 0 | 4 | 2 | 1 | F | x | 2 |
| | <i>Cyclosa conica</i> (PALLAS, 1772) | | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 3 | 1 | F | x | 2 |
| | <i>Gibbaranea</i> sp. | | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | - | - | - | - | - |

| | | | | | | | | | | | | | | | | | | |
|----------------------------------------------------|-----------------------------------------------------|----|----|----|----|----|----|----|----|----|----|----|-----|---|------|------|--------|--------|
| <i>Mangora acalypha</i> (WALCKENAER, 1802) | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 2 | 1 | 0 | x | 2 | | | |
| <i>Clubionidae</i> (Clu) | | | | | | | | | | | | | | | | | | |
| <i>Clubiona marmorata</i> (L.KOCH, 1866) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | na | 0 | F | n.a. | 2 | | |
| <i>Clubiona</i> sp. | 1 | 1 | 3 | 0 | 0 | 0 | 0 | 11 | 1 | 0 | 0 | 17 | - | - | - | - | | |
| <i>Clubiona subsultans</i> (THORELL, 1875) | 2 | 0 | 0 | 2 | 0 | 0 | 5 | 4 | 0 | 2 | 15 | 3 | 0 | F | x | lm-2 | | |
| <i>Clubiona terrestris</i> (WESTSTRING, 1862) | 9 | 1 | 7 | 2 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 21 | 3 | 0 | G | x | ll,g | |
| <i>Cicurina cieur</i> (FAB- RICIUS, 1793) | 6 | 8 | 5 | 1 | 3 | 1 | 1 | 0 | 0 | 1 | 0 | 26 | 3 | 1 | G | mid | 0-11-2 | |
| <i>Lathys humiliis</i> (BLACKWALL, 1855) | <i>Lathumi</i> | 13 | 10 | 20 | 2 | 1 | 0 | 4 | 15 | 17 | 2 | 4 | 88 | 1 | F | mid | ll,g-2 | |
| <i>Dysderidae</i> (Dys) | | | | | | | | | | | | | | | | | | |
| <i>Harpactea lepida</i> (C.L.KOCH, 1939) | <i>Zelocly</i> | 1 | 1 | 3 | 2 | 0 | 21 | 18 | 0 | 1 | 8 | 23 | 78 | 2 | 0 | F | x | ll |
| <i>Gnaphosidae</i> (Gna) | <i>Zelotes cliviculus</i> (L.KOCH, 1870) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 2 | 5 | - | - | - | - | |
| <i>Hahniiidae</i> (Hah) | <i>Zelotes</i> sp. | 0 | 0 | 0 | 1 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 4 | 1 | 1 | F | h | 0-11 |
| <i>Cryphoeca silvicola</i> (C.L.KOCH, 1834) | <i>Hahnpusi</i> | 0 | 7 | 39 | 0 | 2 | 3 | 25 | 0 | 5 | 0 | 22 | 103 | 1 | 1 | G | h | ll,g,m |
| <i>C.L.KOCH 1841)</i> | <i>Hahnia</i> sp. | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 4 | - | - | - | - | - | |
| <i>Linyphiidae</i> (Lin) | <i>Agyrta conigera</i> (O.P.-CAMBRIDGE, 1863) | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 5 | 1 | 1 | F | h | ll |
| <i>Agyrta ramosa</i> (JACKSON, 1912) | <i>Agyrnomo</i> | 15 | 42 | 22 | 20 | 33 | 30 | 17 | 6 | 6 | 1 | 0 | 192 | 1 | 1 | F | h | ll,g |
| <i>Ashenarius helveticus</i> (SCHENKEL, 1936) | 0 | 4 | 0 | 3 | 3 | 2 | 9 | 2 | 0 | 0 | 2 | 25 | 1 | 1 | G | h | 1 | |
| <i>Bathyphantes nigrinus</i> (WESTSTRING, 1851) | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | F | h | ll-2 | |

Table A1. Continued.

| Family | Species | Abbr. | 1999 | | | 2000 | | | 2001 | | | Σ | | | SC | Web | HAB | MD | STR |
|--------|----------------------------------------------------------------|-------|------|---|----|------|---|-----|------|---|-----|-----|----|----|-----|-----|-----|--------|------|
| | | | | | | C | F | CC | C | F | CCB | CCS | C | F | CCB | CCS | | | |
| | | | C | F | CC | C | F | CCB | C | F | CCB | CCS | C | F | CCB | CCS | | | |
| | <i>Bathyphantes parvulus</i> (WESTRING, 1851) | | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | O | eu | ll,g,2 | |
| | <i>Centromerus aequalis</i> (C.L. KOCH, 1841) | | 0 | 8 | 8 | 0 | 2 | 0 | 0 | 0 | 2 | 0 | 0 | 20 | 1 | 1 | F | h | ll |
| | <i>Centromerus arcamus</i> (O.P.-CAMBRIDGE, 1873) | | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 1 | O | h | lm | |
| | <i>Centromerus incitum</i> (L.KOCH, 1881) | | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 1 | 1 | F | x | ll,m | |
| | <i>Centromerus pubulator</i> (O.P.-CAMBRIDGE, 1857) | | 1 | 1 | 5 | 0 | 2 | 0 | 0 | 0 | 5 | 1 | 0 | 15 | 2 | 1 | G | x | ll,g |
| | <i>Centromerus sylvaticus</i> (BLACKWALL, 1841) | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 2 | 3 | 2 | 1 | F | h | ll,g,2 | |
| | <i>Ceratinella brevis</i> (WIDER, 1834) | | 3 | 3 | 2 | 1 | 0 | 1 | 0 | 2 | 2 | 0 | 1 | 15 | 1 | 1 | F | h | ll,g |
| | <i>Ceratinella scabrosa</i> (O.P.-CAMBRIDGE, 1871) | | 0 | 5 | 6 | 0 | 1 | 1 | 15 | 0 | 0 | 0 | 28 | 1 | 1 | F | h | ll | |
| | <i>Dicyphium cf brevi-</i> <i>setosum</i> (LOCKET, 1962) | | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | na | 1 | O | eu | 1 | |
| | <i>Dipocephalus latifrons</i> (O.P.-CAMBRIDGE, 1863) | | 1 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 1 | 1 | F | h | ll,g | |
| | <i>Diplostyla concolor</i> (WIDER, 1834) | | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 1 | G | h | ll,g,2 | |

| | | | | | | | | | | | | | | | | | |
|---------------------------------------------------------------|----|----|----|----|-----|----|----|----|----|----|----|-----|---|---|---|-----|---------|
| <i>Dismodicus elevatus</i> (C.L. KOCH, 1838) | 0 | 2 | 1 | 1 | 4 | 1 | 2 | 1 | 4 | 0 | 2 | 18 | 1 | 1 | F | x | 2 |
| <i>Drapetisca socialis</i> (SUNDEVALL, 1832) | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 4 | 2 | 1 | F | h | 1-2 |
| <i>Ennelecara congenera</i> (O.P.-CAMBRIDGE, 1879) | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 3 | 1 | 1 | F | h | lg-2 |
| <i>Erigone aura</i> (BLACKWALL, 1841) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 2 | 1 | 1 | O | eu | lg |
| <i>Erigone dentipalpis</i> (WIDER, 1834) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 4 | 1 | 1 | O | eu | lg |
| <i>Gongylidiellum latebricola</i> (O.P.-CAM- BRIDGE, 1871) | 21 | 32 | 4 | 26 | 43 | 12 | 9 | 9 | 14 | 0 | 0 | 170 | 1 | 1 | G | mid | 1lg,m |
| <i>Leptophantes minutus</i> (BLACKWALL, 1833) | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 3 | 2 | 1 | F | eu | 1-2 |
| <i>Leptophantes zimmermanni</i> (BERTKAU, 1890) | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | F | h | 11 |
| <i>Linyphia hortensis</i> (SUNDEVALL, 1830) | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 2 | 1 | F | h | 1lg-2 |
| <i>Linyphia triangulans</i> (CLERCK, 1757) | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 3 | 1 | G | x | 1lg-2 |
| Linyphiidae sp. | 63 | 85 | 67 | 74 | 121 | 80 | 93 | 24 | 44 | 11 | 14 | 676 | - | - | - | - | - |
| <i>Macrargus rufus</i> (WIDER, 1834) | 2 | 1 | 7 | 3 | 7 | 2 | 2 | 2 | 2 | 0 | 0 | 28 | 2 | 1 | F | x | 1lg,m-2 |
| <i>Meioneta affinis</i> (KULCZYNSKI, 1898) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | O | x | 1u,g-2 |

Table A1. Continued.

| Family | Species | Abbr. | 1999 | | | 2000 | | | 2001 | | | Σ | | | SC | Web | HAB | MD | STR |
|--------|-----------------------------------------------------------------|-----------------|------|---|----|------|----|-----|------|----|----|---|----|-----|-----|-----|-----|----|----------|
| | | | | | | | | | | | | | | | | | | | |
| | | | C | F | CC | C | F | CCB | CCS | C | F | C | F | CCB | CCS | | | | |
| | <i>Meioneta rurestris</i> (C.L. KOCH, 1836) | | 0 | 0 | 0 | 0 | 0 | 3 | 6 | 0 | 0 | 3 | 9 | 21 | 1 | 1 | O | x | 11,g,m,u |
| | <i>Micrargus herbigradus</i> (BLACKWALL, 1854) | <i>Micrherb</i> | 8 | 7 | 9 | 14 | 11 | 7 | 7 | 10 | 0 | 1 | 81 | 1 | 1 | F | mid | | 11,g,m |
| | <i>Minytiolus pusillus</i> (WIDER, 1834) | | 0 | 2 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 4 | 1 | 1 | F | x | | 11 |
| | <i>Moehelia penicillata</i> (WESTRING, 1851) | | 1 | 0 | 0 | 0 | 6 | 1 | 0 | 0 | 0 | 0 | 8 | na | 1 | F | x | | 2 |
| | <i>Monocephalus fuscipes</i> (BLACKWALL, 1836) | | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | F | h | | 11 |
| | <i>Neriene peltata</i> (WIDER, 1834) | | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 2 | 2 | 1 | F | x | | 2 |
| | <i>Neriene radiata</i> (WALCKENAER, 1842) | | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 3 | 1 | G | x | | 11,g,2 |
| | <i>Obscuriphantes obscu-</i> <i>rus</i> (BLACKWALL, 1841) | | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | F | h | | 11-2 |
| | <i>Oedothorax apicatus</i> (BLACKWALL, 1850) | | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 11 | 2 | 18 | 1 | 1 | O | eu | | 1u,g |
| | <i>Panamomops affinis</i> (MILLER & KRAT- OCHVIL, 1939) | | 5 | 0 | 0 | 6 | 0 | 0 | 1 | 0 | 0 | 0 | 13 | 1 | 1 | G | x | | na |
| | <i>Pelecopsis elongata</i> (WIDER, 1834) | | 5 | 1 | 1 | 2 | 3 | 0 | 2 | 1 | 1 | 0 | 0 | 16 | 1 | 1 | F | h | 1 |

| | | | | | | | | | | | | | | | | | | |
|-----------------------------------------------------------|-----------|-----|-----|-----|----|----|----|----|----|----|---|----|-----|---|----|--------|----------|----|
| <i>Pocadicnemis pumila</i> (BLACKWALL, 1841) | 0 | 0 | 1 | 0 | 0 | 0 | 7 | 0 | 0 | 0 | 8 | 1 | 1 | O | eu | ll,g,m | | |
| <i>Porriomma campbelli</i> (O.P.-CAMBRIDGE, 1894) | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 1 | F | x | 0-11 | | |
| <i>Porriomma montanum</i> (JACKSON, 1913) | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | F | h | ll | | |
| <i>Tapinocyba pallens</i> (O.P.-CAMBRIDGE, 1872) | Tapipall | 220 | 146 | 147 | 21 | 7 | 23 | 17 | 23 | 7 | 4 | 0 | 615 | 1 | F | h | ll,m | |
| <i>Tapinocyba praecox</i> (O.P.-CAMBRIDGE, 1873) | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 3 | 1 | 1 | O | x | lu,g | |
| <i>Tapinopa longidens</i> (WIDER, 1834) | 0 | 2 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 6 | 2 | 1 | F | x | ll,g-2 | |
| <i>Tenuiphantes alacris</i> (BLACKWALL, 1853) | 1 | 0 | 1 | 0 | 3 | 0 | 0 | 7 | 6 | 0 | 0 | 18 | 2 | 1 | F | h | ll | |
| <i>Tenuiphantes flavipes</i> (BLACKWALL, 1854) | Tenuiflav | 6 | 17 | 35 | 20 | 18 | 4 | 0 | 19 | 7 | 2 | 8 | 136 | 1 | F | x | ll,g,m-2 | |
| <i>Tenuiphantes mengei</i> (KULCZYNSKI, 1887) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | G | h | ll,g,m | |
| <i>Tenuiphantes tenebri-</i> <i>cola</i> (WIDER, 1834) | Tenuene | 16 | 45 | 17 | 28 | 50 | 0 | 0 | 11 | 16 | 0 | 0 | 183 | 1 | 1 | F | h | ll |
| <i>Tenuiphantes tenuis</i> (BLACKWALL, 1852) | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 4 | 1 | 1 | O | x | ll,g,m,u | |
| <i>Troxochrus nasutus</i> (SCHENKEI, 1925) | 2 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 2 | 7 | 1 | 1 | F | h | ll,m-2 | |

Table A1. Continued.

| Family | Species | Abbr. | 1999 | | | 2000 | | | 2001 | | | Σ | | | SC | Web | HAB | MD | STR |
|--------------------|------------------------------------------------------------|---------------------|------|----|----|------|---|-----|------|----|----|-----|-----|------|----|-----|------|------|-----|
| | | | C | F | CC | C | F | CCB | CCS | C | F | CCB | CCS | G | h | | | | |
| | | | | | | | | | | | | | | lg,m | | | | | |
| | <i>Walckenaeria alticeps</i> (DENIS, 1952) | <i>Walalti</i> | 23 | 4 | 10 | 6 | 1 | 4 | 1 | 7 | 3 | 0 | 0 | 59 | 1 | G | h | lg,m | |
| | <i>Walckenaeria atroribialis</i> (O.P.-CAMBRIDGE, 1878) | <i>Walcatro</i> | 15 | 21 | 27 | 7 | 8 | 7 | 18 | 17 | 1 | 2 | 130 | 1 | G | h | lg,m | 2 | |
| | <i>Walckenaeria cucullata</i> (C.L. KOCH, 1836) | <i>Walchysd</i> | 9 | 2 | 6 | 6 | 4 | 1 | 0 | 1 | 0 | 0 | 0 | 29 | 1 | F | x | 114 | |
| | <i>Walckenaeria dysderoides</i> (WIDER, 1834) | <i>Walchysd</i> | 9 | 5 | 27 | 11 | 0 | 16 | 26 | 4 | 1 | 2 | 0 | 101 | 1 | F | x | 112 | |
| | <i>Walckenaeria obtusa</i> (BLACKWALL, 1836) | <i>Walobtus</i> | 2 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 2 | 1 | F | x | |
| Lycosidae (Lyc) | <i>Alopecosa puerulenta</i> (CLERCK, 1757) | <i>Alpuer</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 3 | 0 | O | eu | lg | |
| | <i>Alopecosa</i> sp. | <i>Alsp</i> | 0 | 0 | 2 | 0 | 0 | 11 | 0 | 0 | 1 | 2 | 1 | 17 | — | — | — | — | |
| | <i>Alopecosa taeniatia</i> (C.L. KOCH, 1835) | <i>Altaeniatia</i> | 0 | 0 | 1 | 0 | 0 | 5 | 1 | 0 | 0 | 2 | 4 | 13 | na | 0 | G | na. | |
| | Lycosidae sp. | <i>Lycosidae</i> | 0 | 0 | 0 | 10 | 0 | 571 | 8 | 1 | 1 | 97 | 42 | 730 | — | — | — | — | |
| | <i>Pardosa agrestis</i> (WESTRING, 1861) | <i>Paragrestis</i> | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | O | x | |
| | <i>Pardosa amentata</i> (CLERCK, 1757) | <i>Paramentata</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 11 | 4 | 15 | 3 | 0 | O | eu | lg-2 | |
| | <i>Pardosa lugubris</i> (WALCKENAER, 1802) | <i>Parlugubris</i> | 0 | 0 | 0 | 0 | 9 | 15 | 0 | 1 | 15 | 2 | 42 | 2 | 0 | G | h | lg,m | |
| | <i>Pardosa pratagaea</i> (L. KOCH, 1870) | <i>Parpratagaea</i> | 0 | 0 | 0 | 0 | 0 | 51 | 15 | 0 | 0 | 6 | 1 | 73 | 2 | 0 | O | eu | |
| | | | | | | | | | | | | | | | | 1g | | | |

| | | | | | | | | | | | | | | | |
|-------------------------------------------------------|---|----|----|---|---|----|---|---|----|----|----|----|---|----|------------|
| | | | | | | | | | | | | | | | lg,m |
| <i>Pardosa pullata</i> (CLERCK, 1757) | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | O | eu | |
| <i>Pardosa riparia</i> (C.L. KOCH, 1833) | 0 | 0 | 0 | 0 | 3 | 1 | 0 | 0 | 1 | 5 | 1 | 0 | G | h | 1-2 |
| <i>Pardosa</i> sp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 6 | - | - | - | - | - |
| <i>Trochosa</i> sp. | 0 | 0 | 2 | 0 | 0 | 44 | 2 | 1 | 41 | 6 | 96 | - | - | - | - |
| <i>Trochosa terricola</i> (THORELL, 1856) | 0 | 1 | 18 | 1 | 0 | 19 | 5 | 0 | 4 | 12 | 7 | 67 | 3 | 0 | lg,g |
| <i>Xerolycosa nemoralis</i> (WESTSTRÖMG, 1861) | 0 | 0 | 0 | 0 | 4 | 3 | 0 | 0 | 23 | 15 | 45 | 3 | 0 | G | x |
| Philodromidae (Phi) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 6 | 0 | 6 | - | - | - | - |
| <i>Philodromus collinus</i> (C.L. KOCH, 1835) | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 4 | 3 | 0 | F | x |
| <i>Philodromus</i> sp. | 0 | 2 | 1 | 4 | 5 | 3 | 4 | 1 | 0 | 0 | 2 | 22 | - | - | - |
| <i>Dendryphantes rufidus</i> (SUNDEVAALL, 1832) | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 2 | 0 | F | x |
| <i>Euophrys frontalis</i> (WALCKENAER, 1802) | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 2 | 1 | G | x | lg,g,m,u-2 |
| <i>Evarcha arcuata</i> (CLERCK, 1757) | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 3 | 0 | O | eu |
| <i>Evarcha falcatia</i> (CLERCK, 1757) | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 3 | 0 | O | lg-2 |
| <i>Heliophanus cupreus</i> (WALCKENAER, 1802) | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | G | x |
| <i>Neon reticulatus</i> (BLACKWALL, 1853) | 1 | 10 | 13 | 3 | 2 | 0 | 2 | 1 | 7 | 2 | 43 | 1 | 0 | G | h |
| Salticidae sp. | 1 | 1 | 0 | 4 | 0 | 0 | 2 | 0 | 1 | 0 | 9 | - | - | - | - |

Table A1. Continued.

| Family | Species | Abbr. | 1999 | | | 2000 | | | 2001 | | | Σ | | | SC | Web | HAB | MD | STR |
|-------------------------|--------------------------------------------------------------------------------------------|-------|------|---|----|------|---|-----|------|---|---|----------|-----|---|----|------|------|--------|-----|
| | | | | | | | | | | | | | | | | | | | |
| | | | C | F | CC | C | F | CCB | CCS | C | F | CCB | CCS | | | | | | |
| | <i>Salicius zebraeus</i> (C.L. KOCH, 1837) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 2 | 0 | F | x | 2 | |
| | <i>Synageles venator</i> (LUCAS, 1836) | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 2 | 2 | 0 | O | eu | lg | |
| Segestriidae (Seg) | <i>Segestria senoculata</i> (LINNAEUS, 1758) | 0 | 0 | 2 | 1 | 1 | 3 | 0 | 4 | 5 | 0 | 0 | 16 | 3 | 1 | F | x | 2 | |
| Tetragnathidae (Tet) | <i>Metellina segmentata</i> (CLERCK, 1757) synonym: <i>Meta</i> <i>segmentata</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 4 | 4 | 3 | 1 | G | h | ll | |
| | <i>Metellina</i> sp. | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 2 | 4 | — | — | — | — | — | |
| | <i>Pachygnatha degeneri</i> (SUNDEVALL, 1830) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 2 | 2 | 0 | O | eu | lg,m,u | |
| | <i>Tetragnatha pinicola</i> (L. KOCH, 1870) | 2 | 2 | 1 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 8 | 2 | 1 | O | x | 2 | |
| | <i>Tetragnatha</i> sp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 2 | — | — | — | — | — | |
| | <i>Achaearanea lunata</i> (CLERCK, 1757) | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 3 | 2 | 1 | F | h | 2 | |
| Theridiidae (The) | <i>Robertus lividus</i> (BLACKWALL, 1836) | 4 | 3 | 3 | 1 | 0 | 0 | 1 | 3 | 1 | 0 | 1 | 17 | 2 | 1 | F | eu | ll-2 | |
| | Theridiidae sp. | 7 | 2 | 4 | 7 | 3 | 3 | 7 | 4 | 1 | 2 | 3 | 43 | — | — | — | — | — | |
| | <i>Theridion binaculatum</i> (LINNAEUS, 1767) | 0 | 0 | 0 | 3 | 0 | 5 | 0 | 1 | 0 | 0 | 0 | 9 | 1 | 1 | G | x | 2 | |
| | <i>Theridion boesenbergi</i> (STRAND, 1904) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | n.a. | n.a. | ll | |

| | | | | | | | | | | | | | | | | |
|---------------------------------------------------|-----|-----|-----|-----|-----|------|-----|-----|-----|-----|-----|------|----|---|-----|------|
| <i>Theridion inustum</i> (WALCKENAER, 1802) | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 2 | 0 | 4 | 1 | 1 | F | x | 2 |
| <i>Thomisidae</i> (Tho) | | | | | | | | | | | | | | | | |
| <i>Diaea dorsata</i> (FABRICIUS, 1777) | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 2 | 0 | F | mid | 2 |
| <i>Ozyptila trax</i> (BLACKWALL, 1846) | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | G | h | ll,g |
| Thomisidae sp. | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 22 | 3 | 0 | - |
| <i>Xysticus audax</i> (SCHRANK, 1803) | 4 | 0 | 3 | 0 | 1 | 1 | 4 | 3 | 1 | 5 | 0 | 22 | 3 | 0 | G | x |
| <i>Xysticus cristatus</i> (CLERCK, 1857) | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 4 | 3 | 0 | O | x |
| <i>Xysticus kochii</i> (THORELL, 1872) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 19 | 5 | 24 | 3 | 0 | O | x |
| <i>Xysticus lanio</i> (C.L. KOCH, 1835) | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 3 | 0 | F | h | 3-4 |
| Xysticus sp. | 4 | 7 | 10 | 4 | 12 | 1 | 6 | 5 | 8 | 4 | 0 | 61 | - | - | - | - |
| Not classified | nd | nd | nd | 2 | 8 | 29 | 8 | 8 | 17 | 7 | 4 | 83 | - | - | - | - |
| Individuals | | | | | | | | | | | | | | | | |
| All Individuals | 859 | 958 | 908 | 623 | 741 | 1120 | 592 | 376 | 339 | 344 | 241 | 7101 | | | | |

Treatment: C = control; F = female; CC = clear-cut; CCB = clear-cut beech; CCS = clear-cut spruce. nd = not determined. Size classes of females: 1 = 0-3.0 mm, 2 = > 3.0-6.0 mm, 3 = > 6.0-10.5 mm, 4 = > 10.5 mm; web classes: 1 = with web, 0 = no web; habitat categories: F = open habitats, G = generalist; humidity categories: h = hygrophilic (in wet and humid habitats), mid = in mid humid / mid dry habitats, eu = eurycious (independent of humidity), x = xerobiont-/phil (in dry habitats); stratum categories: 0 = underground living (below stones, caves, etc.), 1 = epigaeic living (ground-dwellers), 1 g = in grass mulches, ll = in forest litter, 1 m = in moss, lu = on uncovered places (bushes trees etc.) Species printed in bold comprised more than 1% of individuals of the total sample.

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