

Rapid changes in butterfly communities following the abandonment of grasslands: a case study

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Abstract. 1. Abandonment of grasslands is a major threat for the conservation of biodiversity in Europe. The response of butterflies towards secondary succession has been studied in northern temperate grasslands, but always by comparing sites at different seral stages.

2. Here, we present a trajectory study based on the monitoring of butterflies from a series of abandoned grasslands in northeast Spain. One additional meadow was traditionally managed for the whole 8-year sampling period and provided a useful control. Both general changes at the community level and species population trends were documented through standardised transect counts.

3. The increase in turf height was neither accompanied by an increase in butterfly diversity nor by consistent trends in body size, dispersal ability and host-plant specialization. However, there was a significant decrease in habitat specialization, consistent with the hypothesis that richness in generalist herbivores is more dependent on biomass production than on plant richness. The number of generations decreased, in line with the hypothesis that species living in habitats subjected to greater disturbance need higher reproductive rates.

4. Butterfly communities underwent substantial changes, as indicated by composition similarity and species population trends. Grassland specialists were forced to disperse from the abandoned meadows and search for refugial habitats, allowing the establishment of new populations in the contiguous managed meadow.

5. Our study shows that grassland abandonment had immediate strong effects on butterflies, acting as an excellent indicator of habitat change. It also points out to the substitution of grassland specialists by common butterflies, less important for conservation purposes.

Key words. Butterflies, community structure, grasslands, life-history traits, population trends, secondary succession.

Introduction

Current transformations in agricultural landscapes are recognised as one of the major causes of decline in biodiversity in Europe (Krebs *et al.*, 1999). Two opposing forces underlie this transformation: agricultural intensification in productive regions

(Benton *et al.*, 2003) and the abandonment of traditional land uses such as grazing and mowing in less productive regions (Strijker, 2005). To reverse this negative trend, agri-environmental schemes have begun to be implemented across Europe (Kleijn & Sutherland, 2003). In northern Europe, where the problem of abandonment has been particularly severe (e.g. Pärtel *et al.*, 1999; Eriksson *et al.*, 2002; Luoto *et al.*, 2003), much effort is now being devoted to halting secondary succession and to restoring abandoned grasslands (e.g. Mortimer *et al.*, 1998; Rosén & van der Maarel, 2000; Pöyry *et al.*, 2004).

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Over the last two decades a number of studies have explored the response of butterfly communities to secondary succession (Steffan-Dewenter & Tschamtkke, 1997; Balmer & Erhardt, 2000; Sanford, 2002; Öckinger *et al.*, 2006; Pöyry *et al.*, 2006). In all cases, a synchronous approach has been followed, in which butterfly communities at different sites representing various seral stages have been compared at the same time (i.e. a snapshot study, *sensu* Diamond, 1986). As a general outcome, these studies have found that butterfly diversity increases at the beginning of succession, but decreases in later stages. However, while the earlier and more conservation-focussed work by Erhardt (1985) and Balmer and Erhardt (2000) highlighted the importance of traditional management of grasslands for butterflies; Steffan-Dewenter and Tschamtkke (1997) and Sanford (2002) were more interested in analysing the trends shown in some ecological traits along succession. In general, they found that body size, dispersal ability and number of generations all decreased as succession progressed. Recent work in northern European countries has explored more in depth the relationship between succession and butterfly diversity. For instance, based on quantitative measurements of disturbance intensity, successional age and mean vegetation height of Finnish meadows, Pöyry *et al.* (2006) suggested that the peak of butterfly species-richness in taller vegetation is indicative of the poorer tolerance of disturbance in insects than in plants. Öckinger *et al.* (2006) also found a positive effect of vegetation height in a comparison between managed, abandoned and restored grasslands in southern Sweden.

Nowadays, butterfly monitoring programmes offer a new possibility for undertaking trajectory studies (i.e. those with temporal replication) to reveal how butterfly communities change in response to plant succession wherever they coincide with sites subjected to successional change. In this paper, such an approach is followed for butterfly communities inhabiting a series of hay meadows in north-eastern Spain that were abandoned (i.e. they were no longer grazed or mown) in the second year of monitoring and started a rapid process of plant succession over the following 7 years. General changes occurring in the composition of butterfly communities (community-level approach), as well as the population dynamics of individual species (species-level approach) are investigated. In addition, we tested the following predictions on expected trends of life-history traits based on previous research: host plant and niche specialization should both increase along a successional gradient (Brown & Southwood, 1983, 1987; Brown, 1985; Brown & Hyman, 1986), while body size (Corbet, 1995; Siemann *et al.*, 1999), dispersal ability and the number of generations should all decrease (Brown & Southwood, 1983, 1987; Brown, 1985).

The aims of this paper are therefore twofold. First, from the perspective of applied ecology, to further document how butterflies respond to grassland abandonment in one of the biologically richest regions in Europe (i.e. the Mediterranean Basin) and second, to improve our understanding of the patterns shown by herbivore communities during secondary succession.

Our work provides further confirmation that butterflies act as good indicators of habitat change.

Material and methods

Study site and butterfly data

This study was carried out in the Aiguamolls de l'Empordà Natural Park (AENP), a reserve of 4784 ha in northeast Spain dominated by agroforestral landscapes and wetlands. In the last 50 years, hay meadows have experienced a dramatic reduction in area and have fallen to about 20% of their former extension due to agricultural improvement and abandonment (Stefanescu *et al.*, 2005). Butterflies have been intensively studied since 1988 as part of the Catalan Butterfly Monitoring Scheme or CBMS (<http://www.catalanbms.org/>). The main objective of this monitoring programme is to produce regional population trends for butterflies. The CBMS applies the method developed for the British Butterfly Monitoring Scheme (Pollard & Yates, 1993), in which visual counts of adult butterflies are conducted regularly along fixed transects, whenever weather conditions meet some specified criteria (see also Van Swaay *et al.*, 2008). In AENP, a transect was started in 1997 at Closes del Tec (42°13'N 3°05'E; see Fig. 1), in the area with the most extensive remnant of traditionally managed hay meadows left in this natural park.

For an 8-year period (from 1997 to 2004), weekly butterfly counts were made along a fixed route of 1122 m from 1 March to 26 September (a total of 30 recording weeks year⁻¹). The transect (Fig. 1) was divided into six sections (length range: 117–286 m), each sampling a different meadow, and all individuals seen within 2.5 m on each side and 5 m in front of the recorder were counted. Meadows were discrete unities separated one from the other by drainage canals and forest hedges,

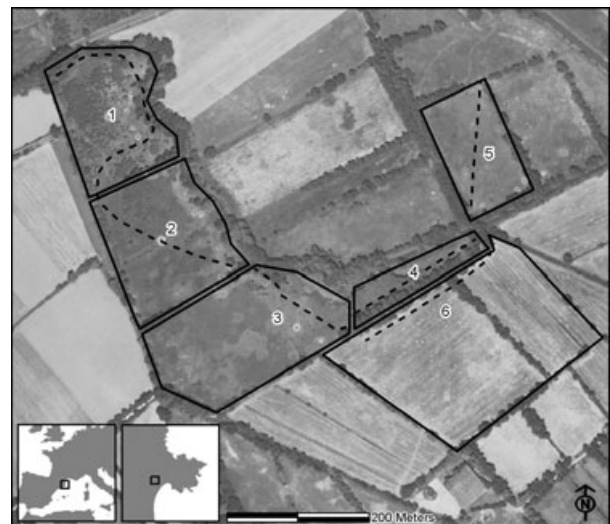


Fig. 1. Study area at Closes del Tec, Aiguamolls de l'Empordà Natural Park, with indication of the butterfly transect (dotted line). Meadows in sections 1–5 were abandoned in the second year of recording (1998), while meadow in section 6 was actively managed (mown in June and grazed by cows and horses in winter) throughout the study period (1997–2004).

and ranged in size between 0.55 and 3.71 ha (average \pm SE 1.87 ± 0.45 ha).

At the end of each season, an annual index of abundance was calculated for each species and each section as the sum of the weekly counts. Data for the few missing weeks (an average of 3.3 weeks year⁻¹) were estimated as the mean of the preceding and succeeding counts, and were included in the calculation of the index of abundance (Pollard & Yates, 1993). Because of the overlapping generations in many multivoltine species, single annual population indices were used. The index of abundance is used to assess change in abundance from one season to the next, on the assumption that a count for a particular species is a more or less constant proportion of the number of butterflies present on the route (for validation of the method, see references in Thomas, 2005).

Assessment of habitat changes

During the first year of monitoring, the six sections of the transect corresponded to two traditional hay meadows mown in June (sections 1 and 5) and four hay meadows mown twice a year, once in June and once in August, which were also grazed by cows in winter (sections 2, 3, 4 and 6). From 1998 onwards, sections 1–5 were abandoned and their vegetation changed dramatically. Grassland cover greatly decreased and was partially replaced by bramble (*Rubus ulmifolius* and *Rubus caesius*) patches and riverine forest. Section 6, on the other hand, remained actively managed (mown and grazed) throughout the study period.

Although no comprehensive record of the succession of plant communities is available, turf-height measurements and flower counts were made in 1997, 2001 and 2004. Turf height was then assessed in June (i.e. near the time of maximum grass growth) with a Boorman disk (Stewart *et al.*, 2001). For each recording year and section, 100 readings were taken on both sides of the transect route. Kruskal–Wallis tests (with Bonferroni correction) were used to test for differences in turf height between years in each section, because data departed strongly from normality even after being log transformed. The relative abundance of flowers was also estimated within the limits of the recording route on five separate occasions (early, mid- and late spring, and early and late summer) in 1997, 2001 and 2004. Following Warren (1985), flower-heads of each plant were ranked from 0 to 4 (0: 0 flower-heads; 1: 1–10; 2: 11–100; 3: 101–1,000; 4: > 1000). For each flower species, total abundance throughout the season was estimated as the sum of the five values estimated from early spring to late summer.

Assessment of changes in butterfly assemblages

Spatial structure in data was tested by means of Spearman correlations of the studied variables between the different sections. Data were significantly correlated in most cases, but there were no differences between proximal and distal sections, i.e. there was no spatial structure. In part, this was because plant communities differed between meadows due to specific

environmental conditions (e.g. soil humidity and salinity, grazing pressure at the starting year of recording, degree of shadow, etc.), which meant that each meadow hosted a particular – albeit rather similar – butterfly community. Moreover, forest hedges and canals acted as moderate barriers for dispersal of sedentary species. Sections 1–5 have therefore been considered as independent samples of a single treatment (abandonment).

Community level. Changes in the structure of butterfly assemblages were investigated by two different approaches. A set of ecological variables were first selected to look for temporal trends by means of linear regression, with years as the independent variable. Generalised linear models (GLM) were used to compare the trends of ecological traits in abandoned versus actively managed sections, considering section as a random variable and time as covariable. Dependent variables were: (i) species richness, (ii) abundance, (iii) commonness (i.e. the complementary of rarity), (iv) body size, (v) generations per year or voltinism, (vi) host-plant specialization, (vii) habitat specialization, and (viii) dispersal ability. The first three are very popular in conservation evaluation (Usher, 1986), while the other five are widely used for analysing patterns in insect communities during plant succession (e.g. Brown, 1985; Steffan-Dewenter & Tschamntke, 1997). Except for species richness and abundance, an overall value for each section and year was calculated as the average of the values of all the species present. Previous to all analyses, the assumption of normality was confirmed by the Kolmogorov–Smirnov test.

Two measures of species richness were employed: (i) all species recorded, and (ii) only those species for which more than one individual was recorded in a given season (i.e. to exclude occasional species or vagrants). Abundance was defined as the number of butterflies recorded per 100 m of transect for all species combined. Commonness was measured at a regional scale as the percentage of CBMS sites located in the Mediterranean region (out of a total of 54) where the species has been recorded; this index thus ranged from 100 (for a very common species present in all 54 sites) to 1.9 (for a very rare species present at only one site). Body size was estimated as the mean forewing length of males (data from Higgins & Riley, 1984). For each section and season the relative contribution (i.e. the proportion) of species having one (univoltine), two (bivoltine) or more (multivoltine) generations per year, as well as the proportion of species feeding as larvae on a single host-plant genus (monophagous), on several genera within a single plant family (oligophagous), or on several genera belonging to a number of plant families (polyphagous) were calculated. Biological data were obtained from Tolman and Lewington (1997) and from personal observations within the study area. Habitat specialization was assessed by means of the *species specialization index* of Julliard *et al.* (2006). Data from the CBMS were used to calculate butterfly densities across 17 different habitat types (see Stefanescu & Traveset, 2009 for details). The degree of habitat specialization was then quantified as the variance of average densities among habitat classes, the coefficient of variation being chosen as a measure of each species' specialization index. Finally, each species was given an index of dispersal according to five categories: 0 – forming

closed populations with very little dispersal; 1 – closed populations with more frequent dispersal; 2 – closed populations with frequent dispersal; 3 – open populations with non-directional dispersal; 4 – open populations with directional migration. Data on dispersal ability and population structure were obtained from various sources (e.g. Pollard & Eversham, 1995; Dennis & Shreeve, 1996; personal observation). The ecological attributes of the butterfly species in the study area are summarised in Stefanescu *et al.* (2005).

A second approach for recording changes was the measurement of how similarities in assemblage composition changed over time (González-Megías *et al.*, 2008). The Morisita-Horn index was used to calculate for each section separately the inter-year similarity between the first year of recording (1997) and all the other years (1998–2004). This index, which is influenced by both the relative abundances of each species and species composition, was calculated using the program ESTIMATES v 7.5 (Colwell, 2005) as:

$$C_{MH} = \frac{2 \sum (a_i \times b_i)}{\left(\sum \frac{a_i^2}{N_a} + \sum \frac{b_i^2}{N_b} \right) N_a \times N_b}$$

where N_a is the total number of individuals in year A , N_b the total number of individuals in year B , a_i the number of individuals of the i th species in year A , b_i the number of individuals of i th species in year B .

Species level. Population trends of the most common 27 butterfly species (i.e. those present in the transect counts in $\geq 75\%$ of the recording seasons) were assessed for each section using the slope of the regression of \log_{10} (annual index of abundance + 1) on years, as in Pollard *et al.* (1998). Because butterfly populations tend to fluctuate in synchrony over large areas as a response to widespread weather factors (e.g. Pollard, 1991; Sutcliffe *et al.*, 1996), both the absolute trend and the relative trend of the site in comparison with wider regional trends were analysed. For calculating the relative trends at the study site, the log indices of the butterflies were regressed against the CBMS collated indices (after excluding data from Closes del Tec) and the residual variation was then regressed on years (Pollard *et al.*, 1998).

The sign and strength of population trends when the habitats change along secondary succession (i.e. the value of the slope regressions) will depend on the habitat preferences and requirements of each species. It is expected that species favouring later seral stages will show positive trends as plant succession leads to more closed conditions in abandoned sections, and that the opposite will occur for typical grassland species favouring open habitats. On the other hand, in the actively managed section no directional trends were expected, as habitat quality will not improve or deteriorate over the longer term. To test these predictions, population trends were regressed against habitat indicator values estimated from a previous principal component analysis (PCA) (see Stefanescu *et al.*, 2005). In that analysis, butterfly species abundance and five habitat variables in six monitoring transects in Aiguamolls de l'Empordà Natural Park were ordinated in a reduced dimensional space. The first axis represented a gradient from woodland habitats (negative values) to

grasslands habitats (positive values). Here, the PCA scores in this first axis are used as a measure of each species' habitat preference.

Generalised linear models were used again to test if any ecological trait (body size, dispersal ability, habitat specialisation, habitat indicator values, host-plant specialization and voltinism) was related to the population trends in the abandoned sections.

Data were tested for normality with SPSS 15.0 (SPSS Inc., Chicago, IL, USA). GLM and regressions were conducted with SPSS 15.0 and STATISTICA 6.0 (StatSoft, Inc., Tulsa, OK, USA) programme packages.

Results

Vegetational changes

Abandoned grasslands experienced striking changes in their vegetation composition and structure. Turf height increased significantly in all five meadows (Kruskal–Wallis tests: $P < 0.001$), as a result of the spread of the coarse grasses *Festuca arundinacea* and *Dactylis glomerata*, which started soon after they were last mown in June 1998 (Fig. 2a). Brambles invaded most sections (Fig. 2b) and, along with a gradual colonisation by ashes *Fraxinus oxycarpa* and white poplars *Populus alba*, caused a rapid encroachment of habitats. This was accompanied by a strong decline and even extinction of Leguminosae (Fig. 2c) and an increase in plants such as *Mentha suaveolens* and the thistles *Cirsium vulgare* and *Cirsium arvense* (results not shown). Because of periodical flooding and a brackish environment, plant succession was slower in section 5; here, sward height only increased significantly between 1997 and 2001 (Fig. 2a). Although no encroachment by trees or brambles (Fig. 2b) occurred in this section, there were dramatic increases in the number of reeds *Phragmites australis* and the previously unrecorded Cruciferae *Brassica nigra*.

In sharp contrast to the abandoned sections, turf height remained stable in section 6 (Kruskal–Wallis test: $P > 0.05$; Fig. 2a). However, this meadow did suffer slightly from encroachment by brambles (Fig. 2b), and there were strong fluctuations in flower abundance (e.g. of Leguminosae; Fig. 2c), most likely attributable to changing climatic conditions during the study period.

Changes in butterfly assemblages

Community level. Trends in ecological traits are summarized in Table 1. Butterfly assemblages in abandoned sections showed strong tendencies to reduce their number of generations, to increase in body size and to decrease in habitat specialization. Commonness increased significantly in only one section and was marginally significant for the pooled data of all five abandoned meadows. On the other hand, there were contrasting trends between sections or no trends at all for species richness, abundance, host-plant specialization and dispersal ability. As expected, in the non-abandoned meadow, there were no changes in life-history traits, although somewhat surprisingly, there were

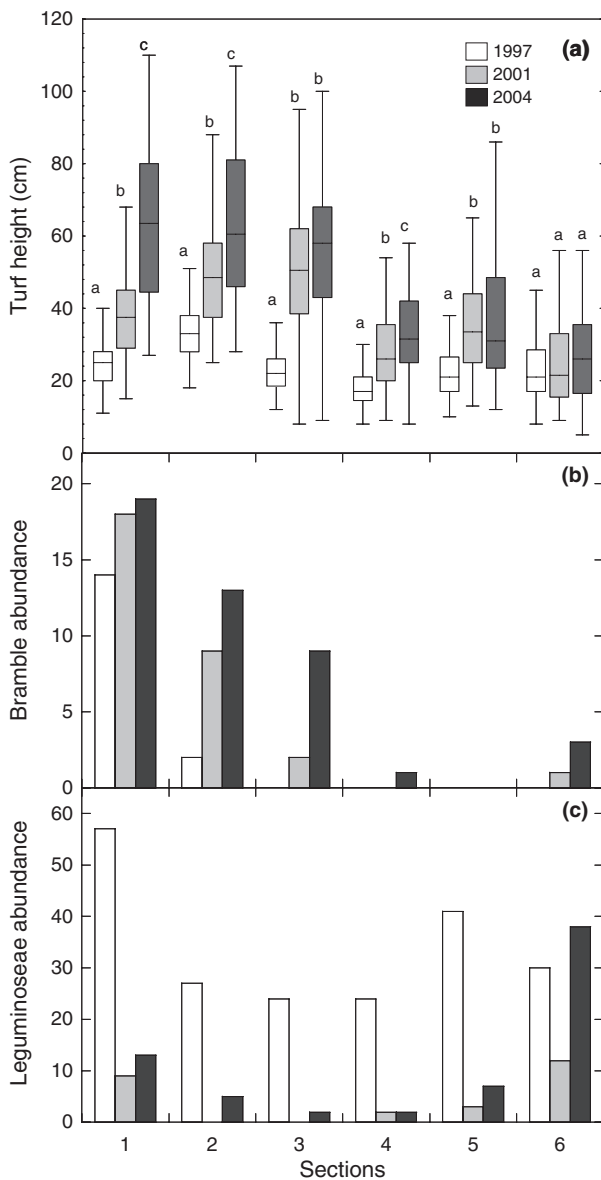


Fig. 2. Changes in the vegetation in monitored meadows. (a) turf height in June. Box-Whisker plots show median and first and third quartile values; different letters refer to significant differences ($P < 0.05$, Kruskal-Wallis tests with Bonferroni correction); (b) abundance of brambles (*Rubus ulmifolius* and *Rubus caesius*); (c) abundance of plants of the family Leguminosae. Turf height was assessed with a Boorman disk, while bramble and Leguminosae abundance was assessed by means of an index of flower abundance based on five separate flower counts each season.

significant increases in the species richness and abundance. However, GLM only showed significant differences between non-abandoned and abandoned meadows for voltinism and habitat specialization (Table 1).

There was also a marked contrast in the pattern of change in community composition depending on treatment (Fig. 3a). In

Table 1. Trends in conservation criteria and ecological traits recorded for butterfly communities in the abandoned (sections 1–5) and the actively managed (section 6) hay meadows during the study period (1997–2004).

Conservation criterion/ ecological trait	Abandoned sections	Managed section	Group* years
	Sections 1–5	Section 6	
Species richness-1	0.2929 $P = 0.481$	0.6865 $P = 0.060$	$P = 0.233$
Species richness-2	0.3873 $P = 0.343$	0.7423 $P = 0.035$	$P = 0.326$
Abundance	0.6616 $P = 0.074$	0.8895 $P = 0.003$	$P = 0.126$
Commonness	0.3110 $P = 0.051$	–0.1625 $P = 0.701$	$P = 0.231$
Body size	0.4461 $P = 0.004$	–0.1219 $P = 0.774$	$P = 0.111$
Voltinism	–0.7226 $P = 0.000$	–0.0049 $P = 0.991$	$P = 0.010$
Host-plant specialization	0.0086 $P = 0.958$	0.1619 $P = 0.702$	$P = 0.715$
Habitat specialization	–0.4764 $P = 0.002$	0.3471 $P = 0.400$	$P = 0.038$
Dispersal ability	0.0539 $P = 0.741$	–0.0432 $P = 0.919$	$P = 0.821$

Trends were tested by linear regression with years as the independent variable, after pooling data for abandoned grasslands. Regression coefficient and P values are shown (significant values in bold). The P value for the GLM comparison between the trends in abandoned and actively managed meadows is presented in the Group* years column. GLM, Generalised linear models.

abandoned meadows, community composition changed markedly during the first 4 years (with a sharp decrease in the Morista-Horn index from 0.90 to 0.41) and then stabilised. The butterfly assemblage in section 6 did not undergo any important changes other than during the last 2 years, when the similarity fell greatly from 0.81 to only 0.50. The reason for this sudden change was the dramatic population increase of *Plebejus argus* (Linnaeus), Lycaenidae, which became the single dominant species. If *P. argus* is excluded, community composition remained much more stable (similarity 0.85 ± 0.026) (Fig. 3b).

Species level. As hypothesised, in abandoned meadows species preferring grasslands showed negative population trends, and species preferring woodland and bramble hedges showed positive trends (Fig. 4). This was confirmed by the negative correlation between population trends and PCA scores ($r = -0.39$, $P = 0.042$), which improved slightly when local trends were controlled for regional trends ($r = -0.43$, $P = 0.035$). However, because succession was still at an intermediate stage, species with mixed habitat preferences (i.e. those occupying a middle position along the x-axis) showed the strongest population increases. Thus, the former pattern was best explained by a curvilinear rather than a linear relationship (absolute trends: $r = 0.55$, $P < 0.002$; relative trends: $r = 0.59$, $P < 0.002$).

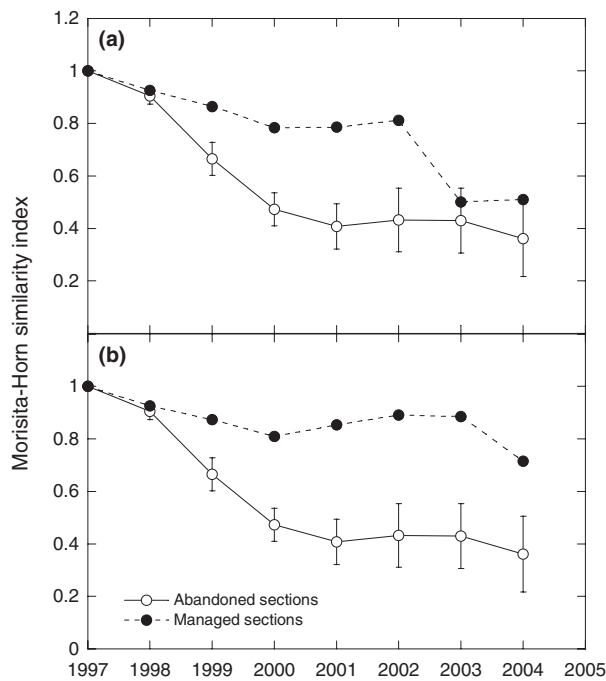


Fig. 3. Morisita-Horn similarity index between the first year of recording (prior to abandonment) and subsequent years (after abandonment) for abandoned grasslands (sections 1–5; mean SE) and the actively managed grassland (section 6): (a) all species and (b) excluding *Plebejus argus*.

(Fig. 4). On the other hand, there was no correlation between population trends and habitat indicator values in the mown and grazed meadow (absolute trends: $r = 0.27$, $P = 0.18$; relative trends: $r = 0.20$, $P = 0.36$). In fact, only three species, including *P. argus*, showed significant trends (all increases) in this section.

Only two variables, habitat preference and voltinism, were selected in GLM models for population trends in the abandoned sections (Table 2). The proportion of variation explained by the models varied between 60% for absolute trends and 54% for relative trends.

Discussion

The succession of butterfly communities in abandoned meadows has been analysed several times, although always in snapshot studies comparing a series of sites each at a different seral stage (Erhardt, 1985; Steffan-Dewenter & Tschamtker, 1997; Balmer & Erhardt, 2000; Sanford, 2002; Öckinger *et al.*, 2006; Pöyry *et al.*, 2006). To our knowledge, the present study is the first based on a trajectory approach, that is, on the systematic recording over a continuous period of time of plant and butterfly communities undergoing successional change. By means of standardized transect counts, reliable data on butterfly abundance were available from five hay meadows that were abandoned in the second year of monitoring, and from another

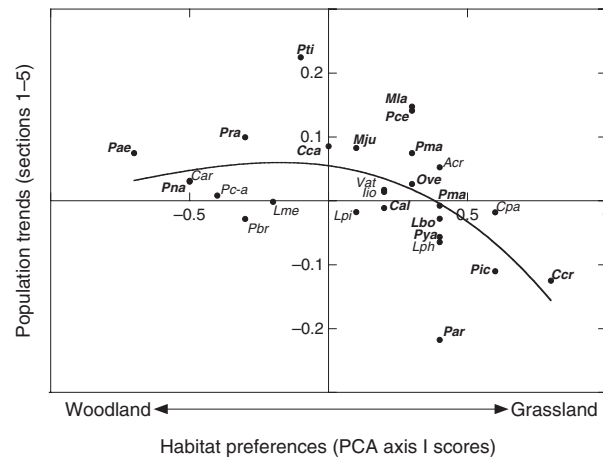


Fig. 4. Absolute trends of the most common butterflies in abandoned grasslands (1997–2004) plotted against habitat indicator values (PCA scores, ordered along a gradient from woodland – negative values – to open grasslands – positive values). Labels in bold type correspond to species showing significant trends in one or more of the abandoned meadows. *Acr*, *Aricia cramera*; *Cal*, *Carcharodus alceae*; *Car*, *Celastrina argiolus*; *Cpa*, *Coenonympha pamphilus*; *Ccr*, *Colias crocea*; *Cca*, *Cynthia cardui*; *Iio*, *Inachis io*; *Lbo*, *Lampides boeticus*; *Lme*, *Lasiommata megera*; *Lpi*, *Leptotes pirithous*; *Lph*, *Lycaena phlaeas*; *Mju*, *Maniola jurtina*; *Mla*, *Melanargia lachesis*; *Ove*, *Ochlodes venata*; *Pma*, *Papilio machaon*; *Pae*, *Pararge aegeria*; *Par*, *Plebejus argus*; *Pbr*, *Pieris brassicae*; *Pna*, *Pieris napi*; *Pra*, *Pieris rapae*; *Pc-a*, *Polygonia c-album*; *Pic*, *Polyommatus icarus*; *Pya*, *Pyrgus armoricus*; *Pma*, *Pyrgus malvoides*; *Pce*, *Pyronia cecilia*; *Pti*, *Pyronia tithonus*; *Vat*, *Vanessa atalanta*.

Table 2. GLM models for population trends of the most common butterflies in abandoned grasslands (1997–2004).

Model	SS type III	d.f.	F	P
(a) Absolute site trends*				
Intersection	0.062	1	17.071	0.000
voltinism	0.094	2	12.899	0.000
PCA score	0.042	1	11.504	0.003
Error	0.084	23		
Total	0.218	27		
(b) Relative site trends†				
Intersection	0.048	1	20.523	0.000
PCA score	0.027	1	11.463	0.003
voltinism	0.037	1	15.615	0.001
Error	0.049	21		
Total	0.117	24		

Separate models are shown for (a) absolute population trends (for the same 27 species as detailed in Fig. 4), and (b) relative trends, i.e. controlled for wider regional trends (for 24 species, after *Plebejus argus*, *Pyrgus malvoides* and *Pyrgus armoricus* were excluded because of insufficient data for calculating regional trends).

* $r^2 = 0.602$.

† $r^2 = 0.540$.

that remained actively managed throughout the whole 8-year sampling period and experienced only minor habitat changes. Population trends could also be controlled for wider regional trends by taking into account a regional index of abundance calculated from other 50 butterfly transects situated within a radius of ca. 300 km of the study site.

Abandoned meadows experienced rapid successional changes, notably a significant increase in turf height as a result of the spread of coarse grasses and the progressive encroachment by brambles and pioneer tree species. Because the diversity of insect herbivores is typically greater in tall than in low vegetation (Lawton, 1983), an increase in butterfly species-richness as succession progressed was expected (cf. Brown & Southwood, 1987). This general trend has been confirmed for butterflies in previous investigations (Erhardt, 1985; Steffan-Dewenter & Tschamntke, 1997; Balmer & Erhardt, 2000; WallisDeVries *et al.*, 2002; Öckinger *et al.*, 2006; Pöyry *et al.*, 2006), but was not observed in our case. The decline in high-quality nectar sources cannot be the reason for this finding because, although some flower species widely used by butterflies disappeared with succession (e.g. several Leguminosae such as *Trifolium pratense*), others increased dramatically in abundance (e.g. *C. vulgare*, *C. arvense*, *M. suaveolens*, *R. ulmifolius* and *R. caesius*). The absence of the expected increase in diversity was most likely a consequence of the rapid loss of plants of the family Leguminosae, on which the larvae of many Lycaenidae, the richest butterfly group in the area, are specialised feeders. On the other hand, a significant decrease in habitat specialization (and a marginally significant increase in commonness) was recorded, a fact that could be explained by the dynamic equilibrium model of Huston (Huston, 1979), which predicts that species richness of specialist herbivores closely follows richness patterns of vascular plants, whereas species richness of generalist herbivores is more dependent on biomass production (see Pöyry *et al.*, 2006). In this respect, the species richness of vascular plants was highest under traditional management (i.e. mowing and light grazing; Gesti *et al.*, 2003), confirming a broad ecological pattern for grasslands (Olf & Ritchie, 1998; WallisDeVries *et al.*, 2002).

Interestingly, both species richness and abundance increased significantly in the single actively managed meadow. These unexpected trends cannot be accounted for as a result of directional changes in the vegetation and most probably were the result of two different processes: first, immigration took place in the form of a number of grassland specialists forced to disperse from the deteriorating meadows and search for refugial habitats in the surroundings fields, and second, as succession progressed some species that prefer more overgrown habitats became very abundant in the abandoned grasslands, making occasional dispersal to other adjacent areas more likely.

Among the life-history traits analysed, a strong decline in the number of generations with succession was found. This result is in accordance with the idea that species living in habitats subjected to greater disturbance (e.g. mown vs. abandoned meadows) need higher reproductive rates to compensate for catastrophic mortality (Brown & Southwood, 1983, 1987; Brown, 1985). Moreover, voltinism remained extremely stable in the actively managed meadow, giving stronger support to this conclusion. A slight but general increase in body size in aban-

doned sections was also found, while dispersal ability remained unchanged, contrary to the predicted patterns (Corbet, 1995; Siemann *et al.*, 1999) and findings of Steffan-Dewenter and Tschamntke (1997) for butterflies. In our case, this was certainly due to the general decline of Lycaenid populations in parallel with the loss of their host plants (see above). Host-plant specialization showed no clear trend, but this was not surprising taking into account the conflicting results found in previous works (cf. Steffan-Dewenter & Tschamntke, 1997). In fact, Steffan-Dewenter and Tschamntke (1997) concluded that this hypothetical relationship is dependent on the plant-insect system studied.

Although only partially revealed by life-history traits, butterfly communities underwent substantial changes in their composition. In abandoned meadows, these changes took place very rapidly in the first 4 years. After this initial rapid faunal turnover, butterfly communities stabilized. These results have interesting conservation implications, as they strengthen the potential use of butterflies as sensible and effective bioindicators of environmental change (Thomas, 2005).

At the species level, directional population changes were more common in abandoned meadows than in the single managed section, a clear evidence of the importance of plant succession as an underlying factor. For some species, the very fast response to the changing environment was an obvious consequence of a change in the availability of larval resources. Thus, for example, *P. argus* became extinct in the abandoned meadows only 3–4 years after the start of the study, in parallel with the disappearance of *L. corniculatus*, on which their larvae feed (Fig. 5). However, in most cases (e.g. most of the Satyrines that feed on several grasses), population changes could not be explained by the presence or absence of larval host plants alone and were more probably a response towards complex changes affecting the whole habitat. This was further demonstrated by the GLM models, which selected habitat preference (defined here as a gradient from woodland to open grassland, with no reference to specific plant composition) and voltinism as the main factors explaining observed population trends. Our results thus show

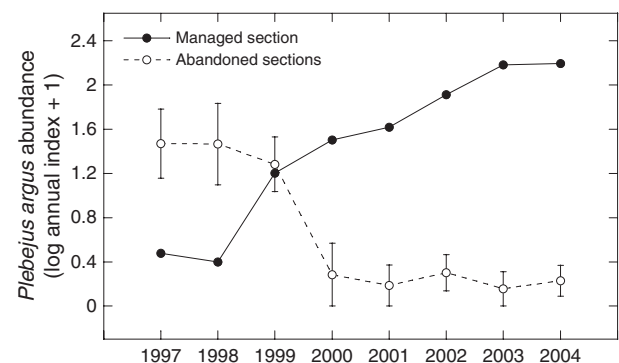


Fig. 5. Population changes of *Plebejus argus* between 1997 and 2004. Populations in encroached meadows (sections 1–5; mean SE) underwent rapid decline and even became extinct after abandonment in 1998. Most likely, habitat degradation encouraged dispersal and favoured the colonization and establishment of a new population in the actively managed meadow (section 6).

that each butterfly species attains an optimum for population growth at some point along the successional gradient, and that this point is strongly conditioned by the number of generations.

A final and quite unexpected result was the important change in the composition of the butterfly community in the actively managed meadow at the end of the monitoring period. Although the detection of additional species was important to a certain extent (see above), the main contributing factor was the colonisation and establishment of a population of *P. argus*, which grew quickly in size to become the dominant species (Fig. 5). When this species was excluded from the calculations, the Morisita-Horn index did not show any marked variation during the sampling period (Fig. 3b). *Plebejus argus* is a classic example of a butterfly that occurs in metapopulations, with populations occupying discrete habitat patches linked by limited adult dispersal (Thomas & Harrison, 1992). Our data strongly suggest that the colonization and establishment of a new population in a vacant patch was related to the decline in habitat quality (due to succession) of nearby occupied patches, which encouraged the dispersal of this otherwise extremely sedentary species (Thomas, 1985).

In summary, this study shows how grassland abandonment has serious and immediate effects on butterflies, adding to the general evidence that this insect group is an excellent indicator of habitat change in terrestrial ecosystems (Thomas, 2005). Moreover, from a conservation point of view, another relevant finding was the observed general decrease in habitat specialization of the butterfly assemblages. This trend reflects the decline of grassland specialists and their eventual substitution by more common and widespread butterflies, less important for conservation purposes.

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