Linking bird, carabid beetle and butterfly life-history traits to habitat fragmentation in mosaic landscapes

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The goal of the present study is to assess how landscape configuration influenced the distribution of life-history traits across bird, carabid beetle and butterfly communities of mosaic forest landscapes in south-western France. A set of 12 traits was selected for each species, characterizing rarity, biogeographical distribution, body size, trophic guild, dispersal power, reproductive potential and phenology. We used a three-table ordination method, RLQ analysis, to link directly bird, beetle and butterfly traits to the same set of landscape metrics calculated in 400 m-radius buffers around sample points. RLQ analyses showed significant associations between life-history traits and landscape configuration for all three taxonomical groups. Threatened species from all groups were characterized by a combination of life traits that makes them especially sensitive to the fragmentation of herbaceous and shrub-dominated habitats at the landscape scale. These key life traits were low productivity, intermediate body mass, restricted geographic range, late phenology and ground gleaning for threatened birds, intermediate body size, spring adult activity, northern distribution and summer breeding period for threatened carabids, and restricted range, overwintering as eggs or larvae, low mobility, monophagy and short flight periods for threatened butterflies. Focusing on species life traits can provide a functional perspective, which helps to determine adequate measures for the conservation of threatened species and communities of several taxonomical groups in mosaic landscapes.

A major consequence of global change on biodiversity is the biotic homogenization of species communities through the gradual replacement of native taxa by non-indigenous species (McKinney and Lockwood 1999). Species communities are thus increasingly composed of generalists, whereas specialists show a general decline (Warren et al. 2001, Kotze and O'Hara 2003, Julliard et al. 2003). At the functional level, declining species are expected to share particular life-history traits, such as large size, low fecundity, rarity, slow dispersal or high specialization, irrespective of taxonomy (McKinney and Lockwood 1999, Cofre et al. 2007). These functional types of species will be affected more than others by habitat loss and fragmentation (Davies et al. 2000, Ewers and Didham 2006). The knowledge of which traits make a species sensitive to habitat fragmentation may consequently be a useful tool for the identification of target groups of species in applied conservation biology (Summerville et al. 2006, Samways and Lu 2007). The following traits have proved to be relevant predictors of species sensitivity to fragmentation: population size and fluctuation, competition and disturbance sensitivity, micro-habitat specialization, matrix use, rarity and biogeographic position (Henle et al. 2004). Other traits such as dispersal ability, body size or trophic position may also predict species response to fragmentation, depending on scale and interactions with other traits (Davies et al. 2000, Baguette and Van Dyck 2007).

Focusing on the distribution of life-history traits across environmental gradients instead of species themselves allows generalizing the results for both theoretical and applied purposes (McGill et al. 2006). Moreover, some authors have stated that ecosystem functioning depends more strongly on functional diversity, i.e. the value and range of species traits, than species richness per se (Diaz and Cabido 2001). Conserving functional diversity at the landscape level may consequently help to maintain large-scale and long-term ecosystem processes by functional compensations between species (Loreau et al. 2003, Tscharntke et al. 2008). As a result, the relevance of life-history trait-based methods to analyze species responses to disturbance is increasingly acknowledged (Söderström et al. 2001, Cole et al. 2002, Summerville et al. 2006). There is actually a need for multiscale and multitaxa approaches taking into account the distinct responses of different species guilds to landscape structure and composition (Grand et al. 2004, Cushman et al. 2008). However, to date few studies have attempted to directly link landscape attributes to the distribution of a set of species life traits (Ribera et al. 2001, Hausner et al. 2003). Here, we examined how landscape structure and composition could

be related to the distribution of bird, carabid beetle and butterfly traits in mosaic landscapes dominated by maritime pine *Pinus pinaster* plantation forests in south-western France.

The maritime pine plantations of south-western France represent a good example of production landscapes harbouring an important animal biodiversity. Previous studies have demonstrated the importance of maintaining semi-natural habitat patches embedded within the pine plantation matrix (firebreaks, heathlands, meadows and deciduous woodlands) for the long-term conservation of threatened species (Barbaro et al. 2007, van Halder et al. 2008). Such "islets" probably act as key habitats (e.g. for feeding, wintering, or breeding requirements) in the life cycle of a large range of sensitive species that may be lost in case of increasing landscape homogenization (Tscharntke et al. 2002, Duelli and Obrist 2003, Purtauf et al. 2005). In plantation forests, management actions should be compatible with the conservation of keystone and threatened species, as well as functional diversity, through the maintenance of a structurally complex landscape matrix including patches and corridors of native vegetation (Fischer et al. 2006). However, little information exists about the management of landscape mosaics for the conservation of several species having contrasting responses to the same landscape configurations (Holzkämper et al. 2006).

In the present work, we aimed at linking directly the distribution of life-history traits in bird, carabid beetle and butterfly communities to the same set of explanatory variables characterizing landscape structure and composition. Our goal was to define functional groups of species sharing similar life traits and similar responses to environmental variables, regardless of their taxonomic status. We performed a set of RLQ analyses, a three-table ordination method that allows a direct ordination of species life traits according to various environmental variables through the link provided by the site × species table (Doledec et al. 1996, Ribera et al. 2001, Hausner et al. 2003, Cleary et al. 2007, Mellado et al. 2008). We used a multitaxa data set collected in the same study area in order to define conservation priorities from a functional, rather than only taxonomical, point of view. Our main objective was to identify, across a wide range of organisms, which combination of life-history traits make species sensitive to habitat loss and fragmentation in mosaic landscapes.

Methods

Study area

The study was located in plantation forests that cover around 1 million ha in the Landes de Gascogne region, south-western France. The landscape is dominated by even-aged stands of native maritime pine with a rotation cycle of 40–50 yr. Such a forest management creates mosaic landscapes composed of even-aged pine stands interspersed with recent clearcuts covered by grassland or heathland vegetation, and fragments of semi-natural habitats. The most important semi-natural elements of the landscape are herbaceous or shrubby firebreaks and remnants of deciduous woodlands dominated by *Quercus robur*, *Q. pyrenaica*

and *Betula pendula* occurring along rivers or as patches of a few hectares. Three areas were selected for species surveys and GIS-mapping of land cover types: Tagon (5000 ha, 44°40′N, 0°57′W), Cestas (8000 ha, 44°44′N, 0°46′W) and Solferino (10 500 ha, 44°08′N, 0°55′W). The nine main land cover types represented in the regional landscape included four stages of the rotation cycle in maritime pine plantations (herbaceous clearcut, shrubby clearcut, young pine (<7 m) and mature pine stands (>7 m)), four semi-natural habitats (hay meadow, herbaceous firebreak, deciduous woodland and deciduous hedgerow), and crops (maize field).

Species surveys

Species surveys were performed using a stratified sampling design according to the main land cover types cited above, except crops that were not sampled (see Barbaro et al. 2007 and van Halder et al. 2008 for a detailed description of the sampling design). We surveyed bird communities at 287 sampling plots using point-counts with unlimited distance (Bibby et al. 2000). Two censuses per year were performed, the first during the early breeding season (early April to mid-May) and the second during the late breeding season (mid-May to late June) in 2002–2003. There was a systematic permutation of first and second census between the two observers involved, in order to eliminate a potential observer effect. Points were established at least 400 m apart to avoid double counting, and each visit lasted 20 min, within 5 h after sunrise and avoiding adverse weather conditions such as strong wind and heavy rain (Bibby et al. 2000). We recorded all birds heard and seen except waterbirds, raptors and aerial feeders (swallows and swifts). We used a semi-quantitative abundance index ranging from 0.5 for a non-singing bird to a maximum score of 5, each territorial male or pair being noted as 1. The maximum score obtained between the two visits was the species abundance index used in further analyses (Hausner et al. 2003).

We sampled carabid beetles at 244 sampling plots using pitfall traps, a standardized sampling method allowing the comparison of ground-dwelling beetle assemblages at different sites when it is not necessary to know the actual species abundances (Rainio and Niemelä 2003). We used removable glass traps (opening diameter = 9 cm, volume = 500 ml) levelled to the soil surface and covered with wood plates supported by four nails to protect traps from rain (Purtauf et al. 2005). Each trap was filled with a solution of quaternary ammonium diluted at 25% and collected every three weeks. Trapping went continuously from April to October in 2002–2003. The number of individuals caught in a given trap during the entire trapping period was pooled for data analyses (Cole et al. 2002).

Butterflies were surveyed in 81 plots using line-transects (Pollard and Yates 1993). Within each plot and along its edge, a 400 m-long and 5 m-wide linear transect was laid out and all butterflies were counted within this strip. Each plot was visited four times (between mid-May and early September of 2004) during appropriate weather conditions (t°C >20, cloudless or just a few clouds and wind speed <5 Beaufort). Butterfly species were identified by sight or

caught and released after determination for species difficult to identify. We pooled the total number of individuals per species over the two transects for each plot (interior and edge) and the four visits for data analyses. Interior and edge counts were summed because we aimed at linking species assemblages and life traits to landscape metrics rather than local habitat variables, and sampling only stand interiors would have underestimated the abundance of several species more abundant at stand edges than in the interiors (Ohwaki et al. 2007).

Life-history traits

We selected a set of 12 life-history traits that were expected to be good predictors of species response to fragmentation for the three taxonomical groups (Henle et al. 2004). We used only traits for which detailed and complete information has been published for all species recorded. Although it was not possible to use the same traits and categories for the three species groups, we aimed at characterizing the main life attributes regarding 1) rarity and biogeographical distribution, 2) trophic guild, 3) breeding parameters, 4) body size or mass, 5) mobility, and 6) phenology (Table 1–3). For the three taxa, we retained four attributes related to rarity, biogeography and conservation status (Kotze and O'Hara 2003): 1) overall population trend at the national level, 2) national and 3) regional rarities, defined as the percentage of national or regional range where the species is present, and 4) biogeographic position of the European range (northern, widespread or southern).

Species conservation status was evaluated with the most updated data available for birds (Julliard and Jiguet 2005) and butterflies (Lafranchis 2000) at the national and regional levels. For carabid beetles, we estimated conservation status (trend and rarity) at the European level using red-list data because complete information was not available at the French national level (Turin 2000), and the regional rarity was defined according to Tessier (2000). Data on other life-history attributes were taken from Cramp et al. (1994) for birds, Turin (2000) and Ribera et al. (2001) for carabids, Bink (1992) and Lafranchis (2000) for butterflies. We used categories defined in Laiolo et al. (2004) for bird foraging techniques, and Tscharntke et al. (2002) for butterfly polyphagy levels. Additional data on butterfly life traits that are relevant at the regional level (regional rarity, local flying period, local polyphagy and host plant categories) were recorded by van Halder and Jourdain (unpubl.). Finally, the number of categories per trait was also partly determined by the number of species that shared the same category, in order to keep a balanced number of species per category (Table 1–3).

Landscape metrics

The three study regions were GIS-mapped (ArcView, ESRI, USA) according to land-use types using aerial colour photographs (summer 2000 and 2002) with a resolution of 50 cm as background layer, followed by field validation. We distinguished 10 land cover types on these maps: the eight surveyed habitats plus croplands and urban areas. The latter type was not used in further analyses because

Table 1. Categories of life-history traits used for bird species.

Bird species traits	Categories	Code
National trend	1. Increasing or stable	T_increa
	2. Recently declining	T_recdec
	3. Long-term declining	T_londec
National rarity (% range)	1. >95%	NR_1
	2. 75–95%	NR_2
	3. <75%	NR_3
Regional rarity (% range)	1. >95%	RR_1
	2. 75–95%	RR_2
	3. <75%	RR_3
Biogeographic position	1. Mediterranean or atlantic	B_south
	2. Widespread	B_widesp
	3. Northern or central	B_north
Foraging technique	1. Ground prober	F_grprob
	2. Ground gleaner	F_grglean
	3. Understory gleaner	F_unglea
	4. Canopy foliage gleaner/hawker	F_caglea
	5. Bark forager	F_barfor
Diet	1. Insectivore	D_insect
	2. Mixed diet	D_mixed
	3. Granivore	D_graniv
Nest location	1. Cavity (tree or others)	N_cavity
	2. Open in tree	N_optree
	3. Open in shrub	N_opshru
	4. Open on ground	N_opgrou
Home-range size	1. Small (<1 ha)	H_small
	2. Medium (1–4 ha)	H_medium
	3. Large (>4 ha)	H_large
Clutch size	1. ≤3 eggs	CS_1
	2. 4 eggs	CS_2
	3. 5–6 eggs	CS_3
	4. ≥7 eggs	CS_4
Body mass (g)	1. ≤14 g	BM_1
	2. 15–24 g	BM_2
	3. 25–49 g	BM_3
	4. ≥50 g	BM_4
Migration status	1. Resident	M_resid
	2. Temperate migrant	M_temmig
	3. Tropical migrant	M_tromig
Average laying date	1. March	L_march
	2. Early April	L_earapr
	3. Late April	L_latapr
	4. Early May	L_earmay
	5. Late May and June	L_latmay

Life trait data taken from Cramp et al. (1994), Söderström et al. (2001), Laiolo et al. (2004), Julliard and Jiguet (2005), Supplementary material, Table S1.

urbanization pressure is still low in these forest-dominated landscapes and the percentage cover of urban areas is negligible. Landscape metrics were calculated within 400 m-radius circular buffers (50.3 ha), from the center of the sampled plots, using Fragstats 3.3 in raster version and a cell size of 2.5 m (McGarigal et al. 2002). As we aimed at relating species life traits to the same landscape metrics for the three sampled groups, we used a distance of 400 m because it is ecologically meaningful for these three taxa (Weibull et al. 2003). A distance of 400 m is actually above the mean foraging or dispersal distances for most bird and carabid species involved in the present study (Riecken and Raths 1996, Paradis et al. 1998, Barbaro et al. 2008). Within each buffer, we calculated the following metrics characterizing both composition and configuration of the landscape: the percentage cover of the nine main land cover types, edge density (in m ha^{-1}), mean patch area (in ha) and the Shannon index of habitat diversity (McGarigal et al. 2002). The selection procedure used for landscape metrics

Table 2. Categories of life-history traits used for carabid beetle species.

Carabid species traits	Categories	Code
European trend	1. Increasing	T_increa
	2. Stable	T_stable
	3. Declining	T_declin
European rarity	1. Non-threatened	ER_nonthr
	2. Threatened	ER_threat
Regional rarity	1. >15 regional data	RR_1
	2. 10–15 regional data	RR_2
	3. 4–9 regional data	RR_3
	4. <3 regional data	RR_4
Biogeographic position	1. Mediterranean or atlantic	B_south
	2. Widespread	B_widesp
	3. Northern or central	B_north
Daily activity	1. Diurnal	A_diurn
	2. Both diurnal/nocturnal	A_both
	3. Nocturnal	A_noctur
Diet	1. Collembola	D_collem
	2. Generalist predators	D_predat
	3. Phytophagous or mixed	D_phyto
Overwintering	1. Imago only	O_imago
	2. Imago and larvae	O_larvae
Body color	1. Black or pale brown	C_black
	2. Metallic	C_metal
Breeding season	1. Spring breeder	S_spring
	2. Summer breeder	S_summer
	3. Autumn breeder	S_autumn
Body size (mm)	1. <6 mm	BS_1
	2. 6–7.9 mm	BS_2
	3. 8–9.9 mm	BS_3
	4. 10–11.9 mm	BS_4
	5. ≥12 mm	BS_5
Wing development	1. Brachypterous	W_brachy
	2. Dimorphic	W_dimor
	3. Macropterous	W_macro
Adult activity period	1. Early spring	P_earspr
	2. Late spring	P_latspr
	3. Summer/autumn	P_sumaut

Life trait data taken from Tessier (2000), Turin (2000) and Ribera et al. (2001), Supplementary material, Table S2.

Table 3. Categories of life-history traits used for butterfly species.

Butterfly species traits	Categories	Code
National trend	1. Stable	T_stable
	2. 1–10% decline	T_dec1
	3. 10–25% decline	T_dec2
	4. 25–55% decline	T_dec3
National rarity (% range)	1. >95%	NR_1
	2. 75–95%	NR_2
	3. <75%	NR_3
Regional rarity (% range)	1. 40–85 local districts	RR_1
	2. 20–40 local districts	RR_2
	3. 1–20 local districts	RR_3
Biogeographic position	1. Mediterranean or atlantic	B_south
	2. Widespread	B_widesp
	3. Northern or central	B_north
Polyphagy level	1. Monophagous	P_monoph
	2. Strongly oligophagous	P_oligo1
	3. Oligophagous	P_oligo2
	4. Polyphagous	P_polyph
Host plant type	1. Grasses	H_grass
	2. Herbaceous dicots	H_dicot
	3. Shrub or tree	H_shrub
Overwintering	1. Eggs or young caterpillar	O_eggs
	2. Mature caterpillar	O_caterp
	3. Chrysalis or imago	O_chrysa
Population density (ind ha^{-1})	1. Low (<4 ind ha^{-1})	D_low
	2. Medium (4–16 ind ha^{-1})	D_medium
	3. High (>16 ind ha^{-1})	D_high
Number of eggs	1. <100 eggs	NE_1
	2. 100–200 eggs	NE_2
	3. 200–400 eggs	NE_3
	4. >400 eggs	NE_4
Wing length (mm)	1. ≤14 mm	WL_1
	2. 15–19 mm	WL_2
	3. 20–24 mm	WL_3
	4. ≥25 mm	WL_4
Mobility	1. Sedentary	M_sedent
	2. Rather sedentary	M_ratsed
	3. Mobile	M_mobile
Flying period	1. 1 generation (spring)	F_1spring
	2. 1 generation (summer)	F_1summ
	3. 2 generations	F_2gener
	4. 3 generations	F_3gener

Life trait data obtained from Bink (1992), Lafranchis (2000) and van Halder and Jourdain (unpubl.), Supplementary material, Table S3.

is fully described in previous works (Barbaro et al. 2007, van Halder et al. 2008).

Data analysis

The methodological question of directly linking life traits of species to environmental variables through the ordination of the species abundance matrix was resolved by Doledec et al. (1996). They named RLQ analysis a generalization of co-inertia analysis (Dray et al. 2003) for analysing the joint structure of three-table data sets where R is the matrix of p environmental variables recorded at m sites, L is the matrix of k species abundances noted at m sites, and Q the matrix of n life traits characterizing the k species (Ribera et al. 2001). In such a design, R, L, and Q tables are linked both by their m rows (sites) and k columns (species), and the ordination of the L-species table represents the link between the R-environment table and the Q-trait table (Doledec et al. 1996). The first step of RLQ analysis is the separate analyses of R, L and Q-tables. The L-species abundance tables of bird, beetle and butterfly species were first analysed by correspondence analyses (CA), after eliminating the rare species recorded with < 10 individuals for birds and < 5 individuals for beetles and butterflies (Ribera et al. 2001,

Cleary et al. 2007). We consequently analysed final data tables of 287 sites × 52 species for birds, 244 sites × 45 species for carabids and 81 sites × 42 species for butterflies.

The R-environment tables were analysed by normed principal correspondence analyses (PCA) with CA site scores used as row weighting to allow the coupling of R and L (Hausner et al. 2003). The Q-trait tables were analysed by multiple correspondence analyses (MCA) using CA species scores for column weighting. When the L-table is analysed by way of a CA, RLQ analysis aims at selecting ordination axes that maximize the covariance between linear combinations of the columns of R- and Q-tables (Doledec et al. 1996). RLQ analysis is a doubly constrained ordination where the stand scores in the R-table constrain the stand scores in the L-table, and the species scores in the Q-table constrain the species scores in the L-table (Hausner et al. 2003). The overall significance of the relationships between landscape variables of the R-tables and species traits of the Q-tables was assessed by a Monte-Carlo test with 1000 permutations on total inertia of the RLQ

analyses (Doledec et al. 1996). We compared the total inertia of the three RLQ analyses with the inertia of unconstrained separate analyses of R, L and Q to evaluate the percentage of the variation in separate analyses taken into account by the RLQ analysis on the main ordination axes (Hausner et al. 2003). RLQ analyses were performed using the "ade4" package in R software (Dray and Dufour 2007).

Results

Birds

There was a significant overall association between bird species traits and landscape variables (permutation test, p < 0.001). The first two axes of RLQ analysis accounted for most of the variance of the corresponding axes in the separate analyses of landscape metrics, species traits and species composition tables (Table 4). The landscape variables that correlated best with the first axis were mean patch area on the negative side and edge density and deciduous wood cover on the positive side (Table 5 and Fig. 1a). It matched a landscape fragmentation gradient from mosaics dominated by large open habitats (young pines, crops and clearcuts) to more diverse mosaics with semi-natural habitat fragments including deciduous woods, hedgerows and meadows. The species traits showing the highest correlation ratios with the first axis were foraging technique, national and regional rarities, nest location and migration status (Table 6). Rare and threatened species (RR_3, NR_3, T_londec) of mid size and low productivity (BM_3, CS_1) having either northern or southern distributions (B_north, B_south) and being mostly ground gleaners and tropical migrants (F_grglean, M_tromig) were associated with the less fragmented open habitats of the younger stages of the silvicultural cycle (Fig. 1b). They included *Anthus campestris* or *Lanius collurio* as typical species (Fig. 1c). Fragmented landscape mosaics with deciduous woods and meadows were associated with ground probers, bark foragers, cavity nesters and early breeders of high productivity, including both large species such as *Turdus merula* and smaller species such as *Parus major* (Fig. 1c). These species are not threatened (T_increa, NR_1, RR_1) and resident or temperate migrants (M_resid, M_temmig).

The second axis was related to a gradient of landscape composition from mosaics including non-forest habitats (crops and meadows) to mosaics dominated by continuous mature plantations (Fig. 1a). The species traits correlated with this axis were foraging technique, clutch size and body mass (Table 6). Small canopy gleaners with high productivity and small home ranges (BM_1, F_caglea, CS_3, H_small) tended to occur in landscapes dominated by continuous pine plantations, whereas large ground foragers or seed eaters with low productivity (CS_1, BM_3, D_graniv, F_grprob) were preferably found in landscapes where plantations are mixed with other non-forest habitats (Fig. 1b). Typical species included *Phylloscopus collybita* or *Parus cristatus* on one side, and *Lullula arborea* or *Streptopelia turtur* on the other side (Fig. 1c).

Carabid beetles

The RLQ analysis showed a significant association between life traits of carabid beetles and landscape variables (permutation test, p < 0.001). The first two axes accounted for a large part of the variance in the separate analyses of environment, traits and species tables (Table 4). The first axis had the highest correlations with edge density on the positive side, and mean patch area and young pine cover on the negative side (Table 5 and Fig. 2a). As with the bird trait analysis, it was related to a gradient of landscape fragmentation. The highest correlation ratios were obtained for regional rarity, biogeography and activity period (Table 6 and Fig. 2b). Regionally common species (RR_1, RR_2) of southern distribution (B_south) and active in summer and autumn (P_sumaut) were associated to fragmented landscapes with deciduous woods (e.g. *Carabus purpurascens* or *Pterostichus madidus*). On the contrary, regionally rare and declining species (T_declin, RR_3, RR_4) of northern distribution (B_north), often active in late spring (P_latspr), were more abundant in less fragmented landscapes with young pine plantations and firebreaks (e.g. *Harpalus rufipalpis* or *Poecilus versicolor*, Fig. 2c).

The second axis of the RLQ analysis was correlated with mature pine cover on the negative side, meadow cover and hedgerow cover on the positive side. This axis was hence similar to the landscape composition gradient obtained for the analysis of bird traits (Fig. 2a). The best correlation ratios for beetle traits on this axis were obtained for body

Table 4. Results of RLQ analyses and comparison with the separate analyses.

RLQ axes	Birds		Carabid beetles		Butterflies	
	F1	F2	F1	F2	F1	F2
Eigenvalue	0.043	0.010	0.206	0.091	0.057	0.040
Covariance	0.207	0.102	0.454	0.302	0.239	0.199
Correlation	0.226	0.152	0.371	0.403	0.266	0.289
R/RLQ	86.3	89.9	89.8	88.5	92.3	86.6
L/RLQ	45.4	40.1	42.1	47.3	43.7	56.0
Q/RLQ	73.5	79.1	60.7	79.2	57.1	67.6

R/RLQ represents the percentage of the variance of the separate analysis of R (landscape variables table) accounted for by each of the first two ordination axes of the RLQ analyses. L/RLQ is the same for the separate analysis of L (species composition table) and Q/RLQ is the same for the separate analysis of Q (species traits table). It is calculated as the ratio of the axis eigenvalue of RLQ analysis on the corresponding axis eigenvalue of separate analysis.
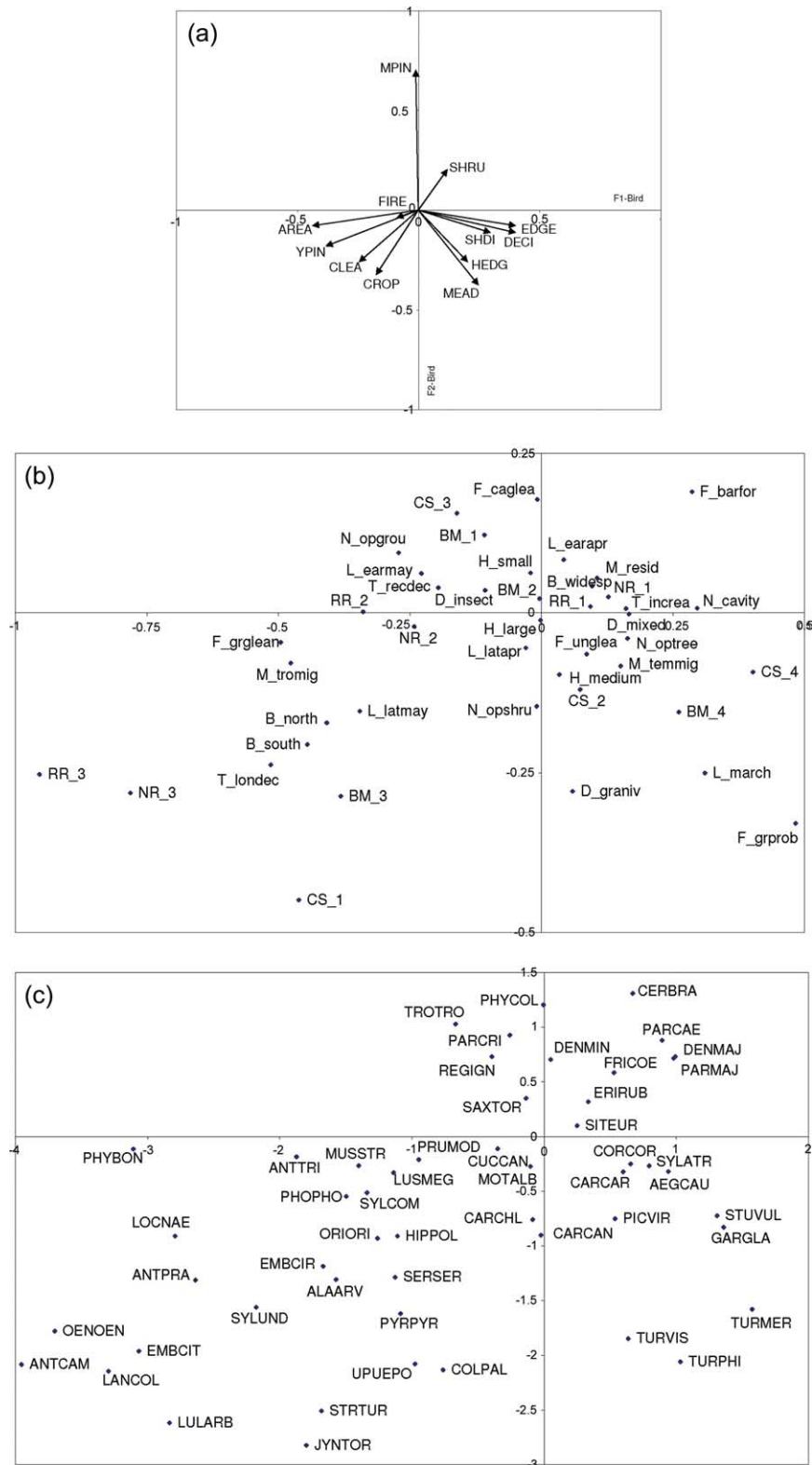
Figure 1. Graphical display of RLQ scores of (a) landscape variables, (b) life traits categories and (c) bird species. See Table 1 and 5 for the codes of life traits and landscape variables respectively. Abbreviations of bird species names use the first three letters of genus and species scientific names, e.g. PHYBON = *Phylloscopus bonelli*. See Supplementary material, Table S1 for a complete species list.

size, diet and breeding season (Table 6). Large predatory and brachypterous autumn breeders (BS_5, D_predat, W_brachy, S_autumn) tended to prefer landscape mosaics dominated by continuous mature pine plantations, whereas small phytophagous and dimorphic spring breeders (BS_4, D_phyto, W_dimor, S_spring) occurred preferably in

Table 5. Correlations between landscape variables and RLQ axes for birds, carabid beetles and butterflies.

Landscape variables	Abbrev.	F1-Bird	F2-Bird	F1-Beet	F2-Beet	F1-Butt	F2-Butt
Edge density (m ha^{-1})	EDGE	**0.41**	0.01	**0.45**	−0.13	**0.46**	−0.07
Mean patch area (ha)	AREA	**−0.43**	0.15	**−0.43**	0.18	**−0.35**	0.11
Shannon diversity index	SHDI	0.30	0.05	0.29	−0.15	**0.43**	0.01
Firebreak cover (%)	FIRE	−0.12	0.01	−0.30	0.29	0.19	−0.02
Meadow cover (%)	MEAD	0.28	**0.38**	0.25	**0.46**	0.06	−0.20
Crop cover (%)	CROP	−0.14	0.33	0.04	−0.01	−0.16	**−0.54**
Clearcut cover (%)	CLEA	−0.24	0.26	−0.09	−0.11	−0.01	0.09
Shrubland cover (%)	SHRU	0.11	−0.25	−0.08	−0.04	**0.48**	0.42
Young pine cover (%)	YPIN	**−0.37**	0.20	**−0.40**	0.22	0.04	0.27
Mature pine cover (%)	MPIN	−0.07	**−0.69**	−0.08	**−0.61**	−0.33	0.13
Deciduous wood cover (%)	DECI	**0.42**	0.09	**0.35**	0.21	0.27	**−0.59**
Hedgerow cover (%)	HEDG	0.23	0.26	0.26	**0.39**	0.04	−0.18

Highest correlation values are indicated in bold.

heterogeneous landscape mosaics including semi-natural herbaceous habitats, such as firebreaks and meadows (Fig. 2b, c).

Butterflies

There was a significant overall association between butterfly life traits and landscape variables (permutation test, p < 0.001). The first two axes of the RLQ analysis accounted for a large part of the variance in the separate analyses of tables (Table 4). The first axis was correlated with shrubland cover, edge density and Shannon diversity index on the positive side, mean patch area and mature pine cover on the negative side (Table 5 and Fig. 3a). The main gradient of landscape structure is therefore slightly different for butterflies than for birds and beetles, opposing landscape mosaics dominated by large and homogeneous mature pine plantations with diverse and fragmented mosaics including open habitats (shrublands and firebreaks). On this axis, national trend, regional rarity, flying period and number of eggs had the highest correlation ratios (Table 6 and Fig. 3b). Nationally declining species with one spring generation or two generations and high egg productivity (T_dec2, F_2gener, NR_2, NE_4, F_1spring) tended to occur in fragmented landscape mosaics with high diversity, whereas regionally rare to common species with three flight generations and mid to low productivity (RR_3, NE_2, F_3gener, RR_1) preferred plantation-dominated mosaics with low habitat diversity and low fragmentation. The first species group included *Euphydryas aurinia* or *Melitaea cinxia*, and the second group included *Coenonympha pamphilus* or *Lasiommata megera* (Fig. 3c).

The second axis matched a landscape composition gradient since it was negatively correlated with deciduous woodland cover and crop cover, and positively with shrubland cover (Table 5 and Fig. 3a). The species traits with highest correlation ratios were overwintering, mobility, biogeography and national trend (Table 6). Large, widespread, polyphagous and mobile species overwintering as chrysalis or imago, and using shrub or tree as host plant (O_chrysa, H_shrub, P_polyph, WL_4, B_widesp, M_mobile, M_ratsed) were associated with landscape mosaics where pine plantations are fragmented by other land uses such as cropland or deciduous woodland (Fig. 3b). This species group typically included *Vanessa cardui* or *Gonep-*

teryx rhamni (Fig. 3c). On the contrary, nationally rare and large-scale declining species with northern or southern distribution, being sedentary, rather small, overwintering as eggs or young caterpillar and flying in one summer generation (T_dec3, B_north, NR_3, O_eggs, M_sedent, WL_2, B_south, F_1summ) were preferably found in landscape mosaics including open habitats created by the silvicultural cycle, i.e. secondary shrublands and young pine plantations (Fig. 3b). Species associated with this group were *Coenonympha oedippus* or *Heteropterus morpheus* (Fig. 3c).

Discussion

The three taxonomical groups showed a consistent pattern in the distribution of life-history traits on the main gradients of landscape structure and composition. RLQ analyses allowed to identify a combination of species traits sensitive to environmental changes that may represent useful indicators of large-scale impacts of human activities, such as forestry and agriculture, on the conservation of biodiversity (Ribera et al. 2001, Hausner et al. 2003, Cleary et al. 2007, Mellado et al. 2008). Habitat fragmentation and composition in the mosaic landscapes of the study area were directly related to species attributes characterizing rarity and biogeography, trophic guild, body size, mobility, reproductive potential and phenology. Moreover, the life attributes related to species conservation status were correlated with the gradients of landscape configuration for the three taxonomical groups studied. Birds of conservation concern showed a consistent and negative response to the landscape-scale fragmentation of open habitats and were largely restricted to landscape mosaics with the highest cover of young pine plantations and clearcuts. They tended to avoid both landscapes dominated by continuous mature pine plantations and fragmented landscapes with high habitat diversity including deciduous woodlands and meadows. They were characterized by low productivity, rather large body mass (25–50 g), restricted biogeographic range (either northern or southern), late phenology, and their foraging technique was mainly ground gleaning. Threatened carabid beetles were likewise restricted to the less fragmented landscape mosaics, preferring those with high cover of young pine plantations and herbaceous firebreaks. As noticed for threatened birds, they avoided
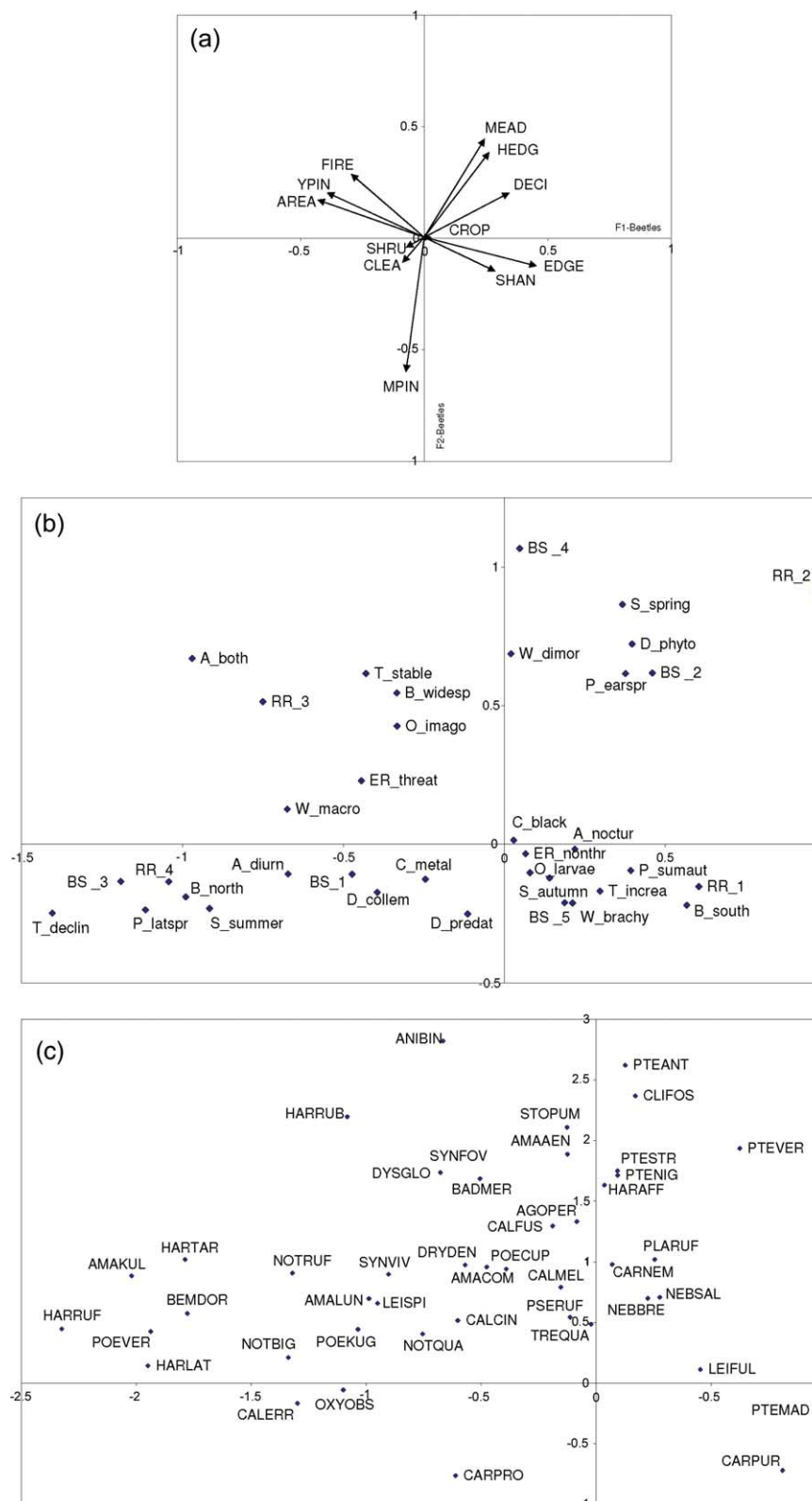
Figure 2. Graphical display of RLQ scores of (a) landscape variables, (b) life traits categories and (c) carabid beetle species. See Table 2 and 5 for the codes of life traits and landscape variables respectively. Abbreviations of beetle species names use the first three letters of genus and species scientific names, e.g. HARRUF = *Harpalus rufipalpis*. See Supplementary material, Table S2 for a complete species list.

continuous mature plantations as well as heterogeneous mosaics with deciduous woods and meadows. These species tended to share intermediate body size, spring adult activity,

northern biogeographic distribution and summer breeding period. The butterflies of highest conservation concern seemed to be less sensitive to landscape fragmentation but

Table 6. Correlation ratios between life traits and RLQ axes for birds, carabid beetles and butterflies.

Bird life traits	F1	F2	Beetle life traits	F1	F2	Butterfly life traits	F1	F2
National trend	0.10	0.04	European trend	0.13	0.14	National trend	**0.27**	**0.18**
National rarity	**0.12**	0.03	European rarity	0.01	0.01	National rarity	0.13	0.16
Regional rarity	**0.12**	0.02	Regional rarity	**0.30**	0.12	Regional rarity	**0.20**	0.07
Biogeography	0.09	0.06	Biogeography	**0.19**	0.14	Biogeography	0.06	**0.24**
Foraging	**0.20**	**0.23**	Daily activity	0.08	0.03	Polyphagy level	0.04	0.09
Diet	0.04	0.05	Diet	0.03	**0.22**	Host plant type	0.07	0.09
Nest location	**0.12**	0.06	Overwintering	0.01	0.05	Overwintering	0.02	**0.33**
Home range	0.01	0.04	Body color	0.01	0.01	Population density	0.15	0.04
Clutch size	0.09	**0.19**	Breeding season	0.08	**0.16**	Number of eggs	**0.17**	0.04
Body mass	0.06	**0.12**	Body size	0.09	**0.24**	Wing length	0.06	0.11
Migration	**0.12**	0.04	Wing development	0.06	0.13	Mobility	0.00	**0.29**
Laying date	0.06	0.11	Activity period	**0.21**	0.11	Flying period	**0.19**	0.09

Highest correlation ratios are indicated in bold.

they depended more on the occurrence of particular habitats, favouring shrublands, young pine plantations and firebreaks against mature pine plantations, crops and deciduous woods. Associated life traits were restricted range, overwintering as eggs or young larvae, low mobility, monophagy and short flight period.

Rarity and biogeography

Species life attributes related to the degree of rarity in a given area, or to the restriction of biogeographical range, have proven to be good predictors of species sensitivity to environmental changes, such as habitat fragmentation (Kotze and O'Hara 2003, Cofre et al. 2007). Species with a restricted distribution range often show strong negative responses to forest fragmentation (Cleary et al. 2007, Ohwaki et al. 2007). However, rare species should be used with care because the rarity of a given taxon is not a good indicator for the occurrence of other rare taxa (Grand et al. 2004). Populations close to the margins of the species range are also more likely to experience long-term declines than those close to the range core (Warren et al. 2001). We found that birds, butterflies and carabid beetles with northern distribution in Europe, and therefore close to their southern range limit in south-western France, favoured landscapes with less fragmented open habitats, i.e. large grasslands and heathlands. These northern species are probably more prone to decline than others in the context of current global change (Julliard et al. 2003, Hampe and Petit 2005). Moreover, the past landscape in the study region was mostly composed of large patches of grasslands and heathlands before the general afforestation process in the middle of the 19th century (Barbaro et al. 2007). The current landscape can therefore be viewed as the result of long-term and large-scale fragmentation of the past open habitats, and homogenization of previously patchy and heterogeneous vegetation, by modern intensive forestry. As elsewhere in Europe where semi-natural grasslands and heathlands have seriously decreased during the last decades, the species with unfavourable conservation status occurring in the study area were mostly grass-shrubland specialists (Söderström et al. 2001, Warren et al. 2001, Duelli and Obrist 2003).

Trophic guild

The use of trophic guilds in understanding species responses to disturbance or habitat fragmentation is widely used by ecologists (Tscharntke et al. 2002, Purtauf et al. 2005, Cleary et al. 2007), although the results obtained are not always consistent with theoretical predictions (Henle et al. 2004). In the present work, bird foraging technique was clearly dependent on landscape configuration. Large ground insectivore gleaners responded negatively to open-habitat fragmentation, whereas ground probers and seed eaters favoured high landscape diversity, including meadows and deciduous woodlands. Granivore abundance is known to increase significantly following human disturbance, whereas large ground insectivores are often negatively affected by grazing or logging (Söderström et al. 2001, Cleary et al. 2007, Tscharntke et al. 2008). For carabid beetles, habitat fragmentation tends to affect predators more strongly than phytophagous species (Davies et al. 2000), which benefit from surrounding landscape diversity, especially semi-natural grasslands (Ribera et al. 2001, Weibull et al. 2003, Purtauf et al. 2005). We found a similar pattern, with seed-eating carabids being associated with meadows and deciduous woods in the surrounding matrix. For butterflies, high landscape diversity and presence of shrublands and firebreaks favoured monophagous species, whereas polyphagous species were associated with the presence of crops and deciduous woodlands in the surrounding landscape. This is consistent with other studies showing the higher sensitivity of monophagous butterflies to habitat loss (Tscharntke et al. 2002, Ohwaki et al. 2007).

Body size and mobility

Body size and dispersal ability may also be good predictors of species sensitivity to landscape fragmentation, although generally interacting with other correlated traits (Henle et al. 2004, Baguette and Van Dyck 2007). Large carabid beetles are known to be more fragmentation-sensitive than smaller species because of their lower dispersal ability (Kotze and O'Hara 2003, Rainio and Niemelä 2003). Large birds are also negatively affected by forest fragmentation (Cleary et al. 2007), although a recent review on
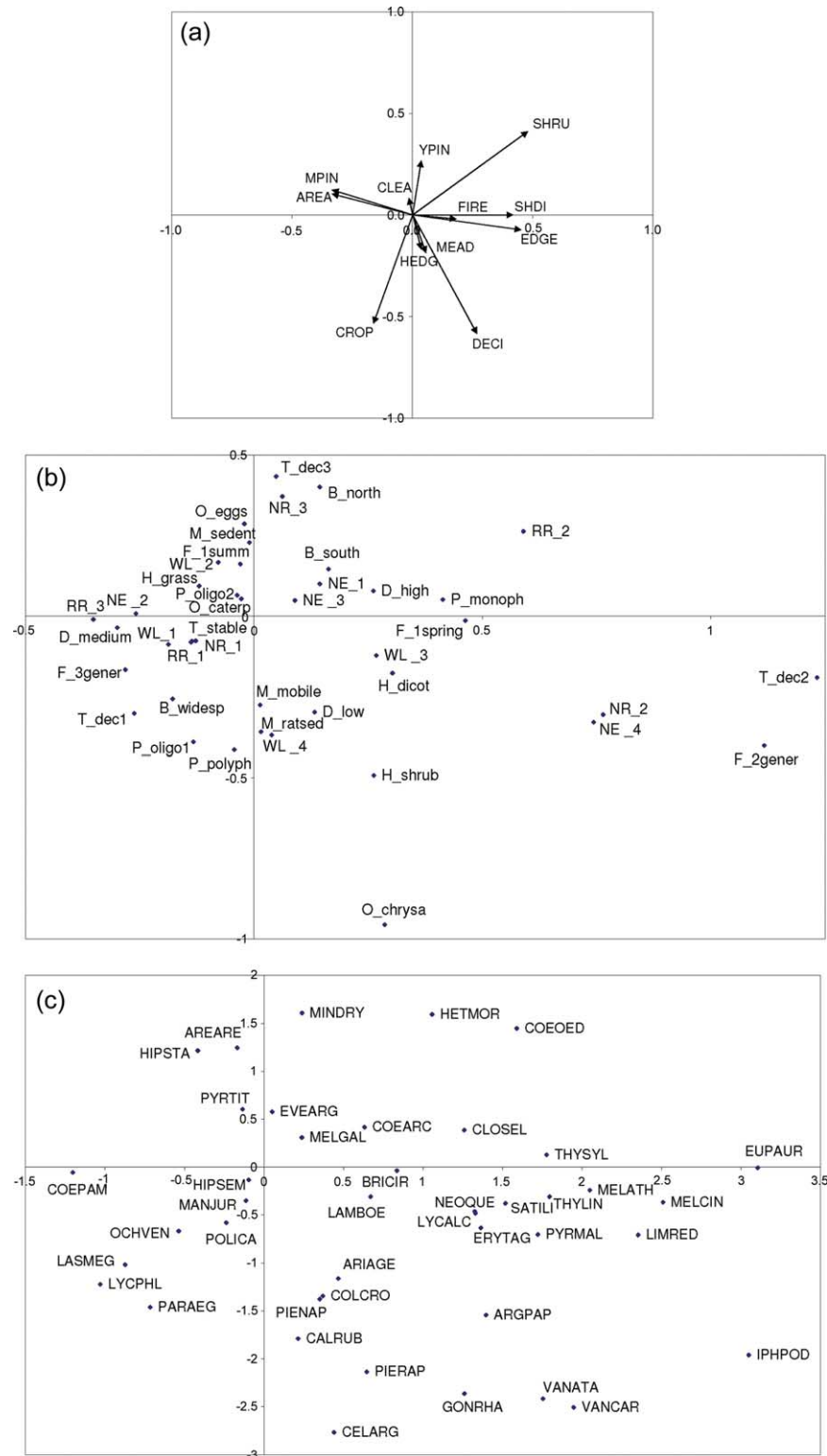
Figure 3. Graphical display of RLQ scores of (a) landscape variables, (b) life traits categories and (c) butterfly species. See Table 3 and 5 for the codes of life traits and landscape variables respectively. Abbreviations of butterfly species names use the first three letters of genus and species scientific names, e.g. MINDRY = *Minois dryas*. See Supplementary material, Table S3 for a complete species list.

tropical agroecosystems failed to detect higher sensitivity to landscape composition in large birds (Tscharntke et al. 2008). Here, we did not detect a negative effect of overall landscape fragmentation on large birds, carabids and butterflies, but instead a positive effect of landscape diversity, the largest species preferring the most diverse landscape mosaics including deciduous woodlands and meadows. However, this is probably due to the naturally

patchy and heterogeneous vegetation in the study area compared to most of the studies dealing with habitat fragmentation.

Long-distance migrating birds and macropterous carabids tended to be more fragmentation-sensitive than their less mobile counterparts (resident and short-distance migrant birds and brachypterous carabids), whereas mobile butterflies were more dependent on landscape composition, especially on the presence of crops and deciduous woodlands. For butterflies and carabids, high mobility is considered to be an adaptation to disturbed habitats and is generally expected to prevent species from decline (Ribera et al. 2001, Warren et al. 2001). However, strong flight can also be a key trait for rare butterflies, as a compensation for extreme habitat specialization and scarcity of the host-plant (Samways and Lu 2007). For birds, long-distance migrants have declined more than short-distance migrants since 1970, indicating higher sensitivity to habitat loss (Sanderson et al. 2006). Greater dispersal ability can lead to greater vulnerability to fragmentation among species, especially in case of greater mortality during dispersal, as demonstrated, e.g. for amphibians (Cushman 2006). Dispersal is however not a species-specific fixed trait but varies with landscape configuration, because mobility can increase in populations inhabiting more fragmented landscapes (Baguette and Van Dyck 2007).

Reproductive potential and phenology

Breeding parameters such as a low reproductive potential may also indicate a higher sensitivity to habitat fragmentation (Henle et al. 2004), and is generally correlated with a large body mass and a low dispersal ability (Kotze and O'Hara 2003, Baguette and Van Dyck 2007). Here we found evidence that birds with both a low productivity and a late phenology were associated with a low fragmentation of open habitats at the landscape scale. For carabid beetles and butterflies, breeding phenology and overwintering mode appeared to be key indicator traits for species responses to landscape configuration. Summer-breeding carabids were associated with low fragmented open habitats, whereas spring breeders were favoured by the presence of meadows and hedgerows. Spring breeders are known to benefit from increasing grassland cover in the surrounding landscape (Weibull et al. 2003), since they usually hibernate as adults, migrate into the fields from surrounding overwintering sites and establish the "early season" carabid community (Purtauf et al. 2005). For butterflies, we found that a restricted flight period and overwintering as eggs or young larvae were good indicator traits for species response to the landscape composition gradient, which is consistent with other studies (Summerville et al. 2006, Ohwaki et al. 2007).

Life-history traits as a tool for conservation

Using life-history traits in the analysis of species responses to fragmentation helps to predict potential changes in ecosystem functioning following changes in the composition of species communities (Diaz and Cabido 2001, Cole

et al. 2002). It also allows to define functional response groups on the basis of shared life traits among species (Ribera et al. 2001, Hausner et al. 2003), and increases our ability to predict why certain species are more prone to decline than others (Henle et al. 2004). As a functional relationship exists between particular habitats and the requirements of species with particular life histories (Duelli and Obrist 2003), life trait-based approaches therefore provide deeper insights into the processes linking species to their habitat (McGill et al. 2006, Summerville et al. 2006). Moreover, many ecosystem functions, including seed dispersal, pollination or biological control, will be affected by changes in bird and insect functional groups following modifications in landscape composition (Tscharntke et al. 2008).

In the study area, some particular landscape configurations need more urgently to be preserved than others because they harbour species sharing a combination of life traits associated with unfavourable conservation status. Maintaining large fragments of grasslands and heathlands is the most adequate conservation issue for threatened species in such mosaic landscapes dominated by silviculture-dependent habitats, whereas the conservation of areas with high landscape diversity will help to maintain high levels of species richness for several taxa. The specific landscape history of the study area (i.e. the large-scale afforestation of naturally fragmented and heterogeneous habitat mosaics by modern forestry) can also explain why positive responses to fragmentation were observed for most forest species (Barbaro et al. 2007). This is also partly due to confounding factors interacting with the fragmentation process per se, especially the ability of surrounding matrix habitats to supply additional resources to forest species by complementation or supplementation, and to regulate dispersal and dispersal-related mortality (Ewers and Didham 2006, Barbaro et al. 2008). Contradictory effects of landscape fragmentation are therefore explained by the different ways in which specialized and generalist species perceive landscape heterogeneity as a continuum of habitat or as isolated patches (Tscharntke et al. 2002). As a result, key indicator traits of species sensitivity to habitat loss and fragmentation might become useful tools for conservation management of mosaic landscapes in the future.

References

Baguette, M. and Van Dyck, H. 2007. Landscape connectivity and animal behavior: functional grain as a key determinant for dispersal. – Landscape Ecol. 22: 1117–1129.

Barbaro, L. et al. 2007. The spatial distribution of birds and carabid beetles in pine plantation forests: the role of landscape composition and structure. – J. Biogeogr. 34: 652–664.

Barbaro, L. et al. 2008. Multi-scale habitat selection and foraging ecology of the eurasian hoopoe (*Upupa epops*) in pine plantations. – Biodivers. Conserv. 17: 1073–1087.

Bibby, C. J. et al. 2000. Bird census techniques. – Academic Press.

Bink, F. A. 1992. Ecologische atlas van de dagvlinders van Noordwest-Europa. – Schuyt and Co.

Cleary, D. F. R. et al. 2007. Bird species and traits associated with logged and unlogged forest in Borneo. – Ecol. Appl. 17: 1184–1197.

Cofre, H. L. et al. 2007. Rarity in Chilean forest birds: which ecological and life-history traits matter? – Divers. Distrib. 13: 203–212.

Cole, L. J. et al. 2002. Relationships between agricultural management and ecological groups of ground beetles (Coleoptera: Carabidae) on Scottish farmland. – Agric. Ecosyst. Environ. 93: 323–336.

Cramp, S. et al. 1994. Handbook of the birds of Europe, the Middle East and North Africa: the birds of the western Palearctic. Vol. I-IX. – Oxford Univ. Press.

Cushman, S. A. 2006. Effects of habitat loss and fragmentation on amphibians: a review and prospectus. – Biol. Conserv. 128: 231–240.

Cushman, S. A. et al. 2008. Do forest community types provide a sufficient basis to evaluate biological diversity? – Front. Ecol. Environ. 6: 13–17.

Davies, K. F. et al. 2000. Which traits of species predict population declines in experimental forest fragments? – Ecology 81: 1450–1461.

Diaz, S. and Cabido, M. 2001. Vive la difference: plant functional diversity matters to ecosystem processes. – Trends Ecol. Evol. 16: 646–655.

Doledec, S. et al. 1996. Matching species traits to environmental variables: a new three-table ordination method. – Environ. Ecol. Stat. 3: 143–166.

Dray, S. and Dufour, A. B. 2007. The ade4 package: implementing the duality diagram for ecologists. – J. Stat. Software 22: 1–20.

Dray, S. et al. 2003. Co-inertia analysis and the linking of ecological data tables. – Ecology 84: 3078–3089.

Duelli, P. and Obrist, M. K. 2003. Regional biodiversity in an agricultural landscape: the contribution of seminatural habitat islands. – Basic Appl. Ecol. 4: 129–138.

Ewers, R. M. and Didham, R. K. 2006. Confounding factors in the detection of species responses to habitat fragmentation. – Biol. Rev. 81: 117–142.

Fischer, J. et al. 2006. Biodiversity, ecosystem function, and resilience: ten guiding principles for commodity production landscapes. – Front. Ecol. Environ. 4: 80–86.

Grand, J. et al. 2004. A multiscale landscape approach to predicting bird and moth rarity hotspots in a threatened pitch pine-scrub oak community. – Conserv. Biol. 18: 1063–1077.

Hampe, A. and Petit, R. J. 2005. Conserving biodiversity under climate change: the rear edge matters. – Ecol. Lett. 8: 461–467.

Hausner, V. H. et al. 2003. Selecting indicator traits for monitoring land use impacts: birds in northern coastal birch forests. – Ecol. Appl. 13: 999–1012.

Henle, K. et al. 2004. Predictors of species sensitivity to fragmentation. – Biodivers. Conserv. 13: 207–251.

Holzkämper, A. et al. 2006. Optimizing landscape configuration to enhance habitat suitability for species with contrasting habitat requirements. – Biol. Conserv. 198: 277–292.

Julliard, R. and Jiguet, F. 2005. Statut de conservation en 2003 des oiseaux communs nicheurs en France selon 15 ans de programme STOC. – Alauda 73: 345–356.

Julliard, R. et al. 2003. Common birds facing global changes: what makes a species at risk? – Global Change Biol. 10: 148–154.

Kotze, D. J. and O'Hara, R. B. 2003. Species decline – but why? Explanations of carabid beetle (Coleoptera, Carabidae) declines in Europe. – Oecologia 135: 138–148.

Lafranchis, T. 2000. Les papillons de jour en France, Belgique et Luxembourg et leurs chenilles. – Biotope.

Laiolo, P. et al. 2004. Can forest management have season-dependent effects on bird diversity? – Biodivers. Conserv. 13: 1925–1941.

Loreau, M. et al. 2003. Biodiversity as spatial insurance in heterogeneous landscapes. – Proc. Nat. Acad. Sci. USA. 100: 12765–12770.

McGarigal, K. et al. 2002. Fragstats: spatial pattern analysis program for categorical maps. – Univ. of Massachusetts.

McGill, B. J. et al. 2006. Rebuilding community ecology from functional traits. – Trends Ecol. Evol. 21: 178–185.

McKinney, M. L. and Lockwood, J. L. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. – Trends Ecol. Evol. 14: 450–453.

Mellado, A. et al. 2008. Biological traits of stream macroinvertebrates from a semi-arid catchment: patterns along complex environmental gradients. – Freshwater Biol. 53: 1–21.

Ohwaki, A. et al. 2007. Butterfly assemblages in a traditional agricultural landscape: importance of secondary forests for conserving diversity, life history specialists and endemics. – Biodivers. Conserv. 16: 1521–1539.

Paradis, E. et al. 1998. Patterns of natal and breeding dispersal in birds. – J. Anim. Ecol. 67: 518–536.

Pollard, E. and Yates, T. J. 1993. Monitoring butterflies for ecology and conservation. – Chapman and Hall.

Purtauf, T. et al. 2005. Landscape context of organic and conventional farms: influences on carabid beetle diversity. – Agric. Ecosyst. Environ. 108: 165–174.

Rainio, J. and Niemelä, J. K. 2003. Ground beetles (Coleoptera: Carabidae) as bioindicators. – Biodivers. Conserv. 12: 487–506.

Ribera, I. et al. 2001. Effect of land disturbance and stress on species traits of ground beetles assemblages. – Ecology 82: 1112–1129.

Riecken, U. and Raths, U. 1996. Use of radio telemetry for studying dispersal and habitat use of *Carabus coriaceus* L. – Ann. Zool. Fenn. 33: 109–116.

Samways, M. J. and Lu, S. S. 2007. Key traits in a threatened butterfly and its common sibling: implications for conservation. – Biodivers. Conserv. 16: 4095–4107.

Sanderson, F. J. et al. 2006. Long-term population declines in Afro-Palearctic migrant birds. – Biol. Conserv. 131: 93–105.

Söderström, B. et al. 2001. Grazing effects on between-year variation of farmland bird communities. – Ecol. Appl. 11: 1141–1150.

Summerville, K. S. et al. 2006. Species traits as predictors of lepidopteran composition in restored and remnant tallgrass prairies. – Ecol. Appl. 16: 891–900.

Tessier, F. 2000. Catalogue des Coléoptères Carabiques du Lot et Garonne. – Bull. Soc. Linn. Bordeaux 28: 1–56.

Tscharntke, T. et al. 2002. Contribution of small habitat fragments to conservation of insect communities of grassland-cropland landscapes. – Ecol. Appl. 12: 354–363.

Tscharntke, T. et al. 2008. Landscape constraints on functional diversity of birds and insects in tropical agroecosystems. – Ecology 89: 944–951.

Turin, H. 2000. De Nederlandse loopkevers. Verspreiding en oecologie (Coleoptera: Carabidae). Nederlandse fauna 3. – Nationaal Natuurhistorisch Museum Naturalis.

van Halder, I. et al. 2008. Importance of semi-natural habitats for the conservation of butterfly communities in landscapes dominated by pine plantations. – Biodivers. Conserv. 17: 1149–1169.

Warren, M. S. et al. 2001. Rapid responses of British butterflies to opposing forces of climate and habitat change. – Nature 414: 65–69.

Weibull, A. C. et al. 2003. Species richness in agroecosystems: the effect of landscape, habitat and farm management. – Biodivers. Conserv. 12: 1335–1355.

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