ORIGINAL ARTICLE

The spatial distribution of birds and carabid beetles in pine plantation forests: the role of landscape composition and structure

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ABSTRACT

Aim To evaluate the joint and independent effects of spatial location, landscape composition and landscape structure on the distribution patterns of bird and carabid beetle assemblages in a mosaic landscape dominated by pine plantation forests.

Location A continuous 3000-ha landscape mosaic with native maritime pine *Pinus pinaster* plantations of different ages, deciduous woodlands and open habitats, located in the Landes de Gascogne forest of south-western France.

Methods We sampled breeding birds by 20-min point counts and carabid beetles by pitfall trapping using a systematic grid sampling of 200 points every 400 m over the whole landscape. Explanatory variables were composed of three data sets derived from GIS habitat mapping: (1) spatial variables (polynomial terms of geographical coordinates of samples), (2) landscape composition as the percentage cover of the six main habitats, and (3) landscape structure metrics including indices of fragmentation and spatial heterogeneity. We used canonical correspondence analysis with variance partitioning to evaluate the joint and independent effects of the three sets of variables on the ordination of species assemblages. Moran's *I* correlograms and Mantel tests were used to assess for spatial structure in species distribution and relationships with separate landscape attributes.

Results Landscape composition was the main factor explaining the distribution patterns of birds and carabids at the mesoscale of 400×400 m. Independent effects of spatial variables and landscape structure were still significant for bird assemblages once landscape composition was controlled for, but not for carabid assemblages. Spatial distributions of birds and carabids were primarily influenced by the amount of heathlands, young pine plantations, herbaceous firebreaks and deciduous woodlands. Deciduous woodland species had positive responses to edge density, while open habitat species were positively associated with mean patch area.

Main conclusions Forest birds were favoured by an increase in deciduous woodland cover and landscape heterogeneity, but there was no evidence for a similar effect on carabid beetles. Fragmentation of open habitats negatively affected both early-successional birds and carabids, specialist species being restricted to large heathlands and young plantations. Several birds of conservation concern were associated with mosaics of woodlands and grasslands, especially meadows and firebreaks. Conserving biodiversity in mosaic plantation landscapes could be achieved by the maintenance of a significant amount of early-successional habitats and deciduous woodland patches within a conifer plantation matrix.

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INTRODUCTION

Depending on scale, the spatial patterns observed in biogeography can be caused by multiple factors. At the continental or regional scale, geomorphological and bioclimatic processes lead to the appearance of gradients and patchy structures, and landscape-scale heterogeneity is dependent on those non-random larger-scale processes (Allen & Starr, 1982). At the local scale, microenvironmental and biotic interactions are the most important factors explaining species distribution patterns, especially within-community richness (Whittaker et al., 2001). At the landscape scale, abiotic factors such as topography, geology or microclimate interact strongly with biotic and human processes such as land use and disturbance regimes, resulting in complex spatial patterns of species occurrence that may be difficult to relate to simple explanatory factors. However, the landscape level is the most relevant scale at which both conservation programmes and the sustainable management of human-piloted ecological systems is practiced (Wiens, 1994). In landscapes dominated by even-aged plantation forests submitted to frequent clearcutting, biodiversity is expected to be a function of spatial heterogeneity created by the mosaic of stands of different age, structure and composition (Tews et al., 2004). In such heterogeneous mosaics, assessment of the effects of matrix composition on biodiversity is best achieved when studying simultaneously several taxonomic groups that respond to different spatial scales, such as birds and insects (Mac Nally et al., 2004; Bossenbroek et al., 2005).

Understanding how landscape composition and structure influence the spatial patterns of species distributions requires the use of methods that take into account both spatial autocorrelation in the data sets and collinearity between explanatory variables (Heikkinen et al., 2004). Including the spatial structure in the modelling of species–environment relationships allows better predictions of species occurrence (Legendre & Legendre, 1998). It also allows one to distinguish when spatial structure is due mainly to biotic interactions, to an underlying unmeasured environmental factor or to a common spatial gradient shared by species data and environmental variables (Borcard et al., 1992). Previous studies have used canonical correspondence analysis with variation partitioning to separate between the confounding effects of space and environmental variation (Hobson et al., 2000; Heikkinen et al., 2004; Titeux et al., 2004; Legendre et al., 2005). Several authors have also separated between the effects of plot-, patch- and landscape-level variables using a multiple-scale hierarchical framework (Saab, 1999; Cushman & McGarigal, 2002; Herrando & Brotons, 2002; Miller et al., 2004; Bossenbroek et al., 2005).

The importance of distinguishing between the effects of landscape composition, as the relative amounts of each habitat type within the landscape mosaic, and landscape structure, as the physical layout of elements within the landscape, was underlined by Dunning et al. (1992). For bird communities, most studies have pointed out a greater effect of landscape composition than landscape structure or configuration, including patch shape, patch isolation and habitat fragmentation (Trzcinski et al., 1999; Drapeau et al., 2000; Cushman & McGarigal, 2002). The type of landscape matrix surrounding a patch can mitigate the negative effect of habitat isolation for a given species, according to its degree of matrix habitat use (Sisk et al., 1997; Estades & Temple, 1999; Norton et al., 2000; Herrando & Brotons, 2002; Lindenmayer et al., 2002). In the case of farmland birds, the occurrence of rare, residual habitats can be the most important factor at the landscape scale (Berg, 2002; Fuller et al., 2004). Two recent studies also suggest that matrix composition has a direct influence on post-disturbance colonization (Brotons et al., 2005) and responses to habitat fragmentation among different landscapes (Watson et al., 2005).

For carabid beetles, habitat type is the most important factor explaining the distribution patterns of species at the regional and landscape scales (Dufrêne, 1992; Aviron et al., 2005; Eyre et al., 2005), but carabid assemblages are mainly affected by microhabitat variation and biotic interactions at smaller scales (Niemelä et al., 1992; Antvogel & Bonn, 2001; Thomas et al., 2001; Brose, 2003). However, studies involving different arthropod taxa in agricultural landscapes suggest that species occurrence in habitat patches and movements between patches are influenced by surrounding matrix composition at the landscape scale (Dauber et al., 2003; Duelli & Obrist, 2003; Weibull et al., 2003; Purtauf et al., 2005).

The aim of this study was to determine the joint and independent effects of spatial location, landscape composition and landscape structure on the distribution patterns of birds and carabid beetles in a 3000-ha landscape sampled with a grid of 400 × 400 m sized squares. We used an intermediate scale between macroscale, where biogeographical factors are expected to be predominant, and microscale where local conditions may influence the spatial distribution of species (Whittaker et al., 2001). First, we decomposed the joint and independent variation in the distribution of species assemblages explained by geographical location of samples, landscape composition and landscape structure using canonical correspondence analysis with variation partitioning (Cushman & McGarigal, 2002; Heikkinen et al., 2004; Legendre et al., 2005). Secondly, we tested for the presence of spatial structure in individual species abundances and examined their correlations with

particular attributes of landscape composition and structure using Moran's *I* correlograms and Mantel tests (Leduc *et al.*, 1992; Legendre & Legendre, 1998; Judas *et al.*, 2002).

We addressed the following questions: (1) is there a spatial structure in the distribution of species assemblages at the landscape scale? (2) What are the joint and independent effects of geographical location, landscape composition and landscape structure on species assemblages? and (3) Can individual species distributions be related to particular landscape composition and structure variables?

METHODS

Study area

The study area is located in south-western France in the Landes de Gascogne region, where an intensive plantation forest of native maritime pine *Pinus pinaster* covers *c.* 10,000 km². We selected a landscape of 3216 ha in size, gathering the catchment areas of two small rivers (Tagon and Aiguemorte, 44°40′ N, 0°57′ E), adjacent to the Arcachon Basin (Fig. 1). The climate is thermo-atlantic (mean annual temperature 12°C, mean annual rainfall 700 mm) and the elevation is low (*c.* 50 m a.s.l.). Soils are mostly podzols established on a sandy substrate (Maizeret, 2005). The eastern part of the area is dominated by a mosaic of maritime pine plantations of different ages, together with clearcuts, heathlands dominated by *Molinia caerulea*, *Pteridium aquilinum*, *Ulex europaeus*, *Erica cinerea*, *Erica scoparia* and *Calluna vulgaris*, meadows and herbaceous linear firebreaks, deciduous forest patches dominated by *Quercus robur*, *Quercus pyrenaica* and *Betula pendula* and linear riparian forest along streams with *Alnus glutinosa* and *Salix* spp. The western part includes large areas of meadows and oak woodlands that are expected to be source habitats for deciduous woodland species (Fig. 1).

Bird and carabid sampling

The overall landscape was divided into 200 squares of 16 ha in size (400 × 400 m). We used a distance of 400 m between sampling points (Weibull *et al.*, 2003) for three reasons: (1) it is *a priori* close to the grain size (mean patch area) of the studied landscape, (2) it is above the auditory detection distance for most bird species sampled by point-counts, and (3) it is also well above the distance of interaction between pitfall traps for the sampling of carabid beetles (Digweed *et al.*, 1995). In each square, we established the sampling point for birds and carabid beetles as close as possible to the centre of the square (Fig. 1).

Bird assemblages were sampled by the point-count method with two visits (Bibby *et al.*, 2000) from early April to mid-May (first visit) and from mid-May to the end of June (second visit) in 2002–03. Two observers performed the surveys and permutated first and second visits for a given point to avoid a possible observer effect. We recorded all birds heard and seen within the square during 20 min (Drapeau *et al.*, 2000), using a semi-quantitative abundance index where a territorial male or pair was noted as 1 and a non-singing bird was noted as 0.5 (Norton *et al.*, 2000). The final abundance index was the maximum score obtained for each species among the two visits. Point counts were performed within 5 h after sunrise and rainy days were excluded. During the count, we mapped the virtual position of each individual bird around the observer to avoid double counting.

Carabid beetles were sampled with the pitfall trap method (Digweed *et al.*, 1995). A systematic grid of 200 traps was established at the same locations as the bird point counts from early spring to late autumn in 2002–03. We used glass traps with a 9-cm diameter opening and a volume of 500 mL, levelled to the soil surface and covered with wood plates supported by four nails to protect traps from rain. We used a solution of quaternary ammonium diluted at 25% to fill the
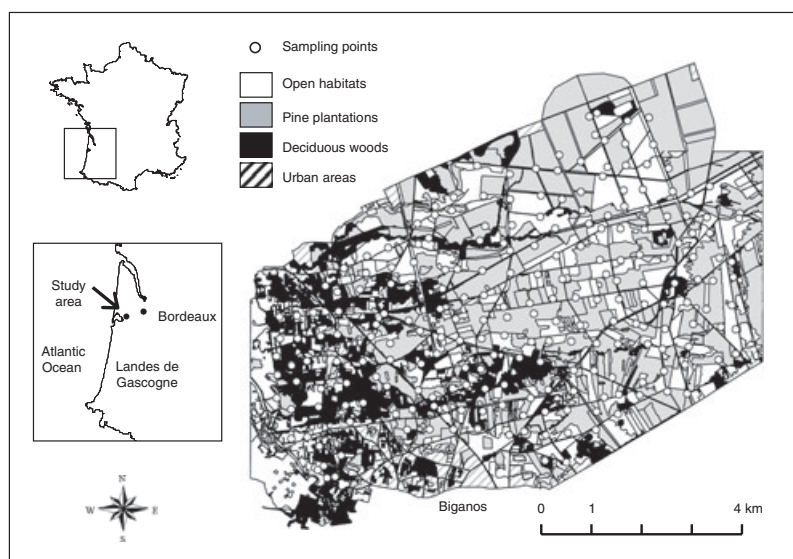

Figure 1 Location map of the study area showing the grid of 200 sampling points.

traps because it is a good preserving fluid even during the high summer evaporation period. Traps were collected every 3 weeks and carabid beetles were identified to species level back in the laboratory. We pooled all individuals captured during the overall period in a given trap for further analyses.

Landscape and spatial variables

The study area was mapped using the GIS ARCVIEW 3.2 (ESRI, Redlands, CA, USA) to obtain for each sampling point three sets of spatial, landscape composition and landscape structure variables. The first set of explanatory variables was composed of five spatial variables: geographical coordinates of the 200 sampling points (x, y) and their squares and cross-product terms (x, y, x^2, y^2, xy) (Wartenberg, 1985). We did not include the cubic terms as proposed by Borcard et al. (1992) to keep a comparable number of factors for the three explanatory data sets.

Habitat mapping was performed using colour aerial ortho-photographs at the scale 1 : 25,000 (Institut Géographique National, June 2000). Habitat type was assigned to each landscape patch according to the following classification, based on structural attributes identified by photo-interpretation and validated by field observation: herbaceous firebreak, heathland, young pine plantation (trees < 7 m), mature pine plantation (trees > 7 m), deciduous woodland and meadow. To calculate the percentage cover of each habitat and the landscape metrics, circular buffered areas of 400-m radius were established around each of the 200 sampling points (Dauber et al., 2003). We used a radius of 400 m (mean distance between sampling points) in order to minimize the spatial overlap between two adjacent buffered areas and consequently to avoid high redundancy of landscape attributes for two close samples. This distance also offered a compromise between the response scale of vertebrate taxa such as birds and invertebrate taxa such as carabid beetles (Barbaro et al., 2005). In preliminary analyses, we also tested the same variables calculated for 200-m radius buffers, but intraset correlations between variables and species were always higher for the distance of 400 m.

In the same buffered areas, we calculated a set of landscape metrics using a raster version of FRAGSTATS 3.3, with a cell size of 2.5 m (McGarigal et al., 2002). We selected the following landscape metrics according to previous studies (Heikkinen et al., 2004): edge density (i.e. total length of all edges between all habitat patches, in m ha^{-1}), mean patch area (in ha), landscape heterogeneity (measured by the Shannon index) and mean shape index (mean of all patch shape indices measured as a ratio of perimeter on area of the patch). As we hypothesized an effect of increasing deciduous woodland cover from the east to the west of the study area, we also calculated the distance to the nearest deciduous wood from each sampling point.

Variance partitioning

For each taxon (birds and carabids) we first performed a direct ordination method, canonical correspondence analysis (CCA), to evaluate the part of the variation in species assemblages that can be explained by the total effect of the three sets of explanatory variables (Legendre & Legendre, 1998). Second, we used partial CCA with variation partitioning to decompose the variance explained by the independent and joint effects of spatial variables, habitat cover and landscape structure (Borcard et al., 1992; Anderson & Gribble, 1998; Heikkinen et al., 2004; Legendre et al., 2005). The significance of each separate analysis was assessed with Monte Carlo permutation tests (2000 permutations) on the total variance explained by each set of explanatory variables, i.e. the percentage ratio of total inertia of each CCA on total inertia of unconstrained CA. To perform partial CCA, we used ADE-4 software by J. Thioulouse, D. Chessel and S. Dolédec, University Lyon 1, 2004 (Thioulouse et al., 1997).

In the case of three sets of explanatory variables, the total explained variance can be partitioned into seven fractions (see below): a, independent effect of habitat cover; b, independent effect of landscape structure; c, independent effect of spatial variables; d, joint effect of habitat and structure; e, joint effect of habitat and space; f, joint effect of structure and space; and g, joint effect of the three sets of variables (Heikkinen et al., 2004). For each taxon, we performed a set of CCA and partial CCA in three steps:

1. CCA of the separate effects of the three explanatory data sets, namely six variables of habitat cover, five variables of landscape structure and five spatial variables;
2. partial CCA of the independent effect of habitat cover with landscape structure and spatial variables as covariables (fraction a), independent effect of landscape structure with habitat cover and spatial variables as covariables (fraction b) and independent effect of spatial variables with habitat cover and landscape structure as covariables (fraction c);
3. partial CCA with elimination of the effect of habitat cover, i.e. the joint effect of landscape structure and spatial variables with habitat cover as covariable (fraction b + c + f), with elimination of the effect of landscape structure (fraction a + c + e) and with elimination of the effect of spatial variables (fraction a + b + d).

We used the following equations for the calculations of fractions d, e, f and g (Anderson & Gribble, 1998; Heikkinen et al., 2004):

$$d = (a + b + d) - (a + b)$$

$$e = (a + c + e) - (a + c)$$

$$f = (b + c + f) - (b + c)$$

$$g = (d + e + g) - (d + e) = (d + f + g) - (d + f)$$
$$= (e + f + g) - (e + f).$$

Spatial statistics

The description of spatial structure (i.e. gradients, patchy structures or random distributions) and the degree of spatial

autocorrelation in single species abundance and landscape variables were assessed by means of Moran's *I* correlograms (Legendre & Legendre, 1998). We used the program ROOKCASE (Sawada, 1999) to calculate the Moran's *I* value for 15 equidistant lags of 400 m (mean distance between two sampling points). A correlogram was considered significant when Moran's *I* was significant at the Bonferroni-corrected probability level $\alpha' = 0.05/15 = 0.0033$ for at least one distance lag, according to a Monte Carlo test with 1000 permutations.

Mantel tests on distance matrices were used as nonparametric tests of association between single species abundance and separate landscape attributes (Legendre & Legendre, 1998). The method is based on distance matrices that contain all the pairwise distances between sampling locations. For species abundance data, Euclidean distances can be used to calculate distance matrices (Leduc *et al.*, 1992). No transformation was applied to bird species abundance because we used a semi-quantitative index ranging from 0 to 5, but we log $(x + 1)$-transformed the number of carabid beetles to normalize the data distribution (Judas *et al.*, 2002). For landscape variables, we used square-root transformation for the distance to the nearest deciduous wood. The statistical significance for Mantel tests was assessed by Monte Carlo tests with 1000 permutations, using the Bonferroni-corrected level of $\alpha' = 0.05/10 = 0.005$.

RESULTS

Ordination of species assemblages

We recorded a total of 76 breeding bird species and 59 carabid beetle species in the 200 sampling points of the study area.

After eliminating the rare species occurring in fewer than five samples for birds and three samples for carabids, species data sets were composed of 53 bird species and 36 carabid beetle species. The total variance explained by the CCA of the three sets of explanatory variables (16 factors) was 24.3% for breeding bird assemblages and 21.4% for carabid beetles, both significant at $P < 0.001$ (Monte Carlo test with 2000 permutations). The first ordination axis for bird assemblages (Fig. 2) was a decreasing gradient from heterogeneous and fragmented landscape mosaics (Shannon index = −0.59, edge density = −0.58) to less fragmented mosaics dominated by heathlands (mean patch area = 0.62, heathlands = 0.65) along a south–north geographical gradient (latitude = 0.63). The second axis was a woodland composition gradient from landscapes dominated by mature pines (−0.86) to landscapes dominated by deciduous woods (0.63). Bird assemblages of heathland-dominated sites were composed of species requiring large areas of open grassy and shrubby habitats: skylark *Alauda arvensis*, red-backed shrike *Lanius collurio*, linnet *Carduelis cannabina*, cirl bunting *Emberiza cirlus*, grasshopper warbler *Locustella naevia* and Dartford warbler *Sylvia undata* (Fig. 2). Redstart *Phoenicurus phoenicurus*, spotted flycatcher *Muscicapa striata*, lesser spotted woodpecker *Dendrocopos minor* and Bonelli's warbler *Phylloscopus bonelli* were associated with deciduous wood cover, while nightjar *Caprimulgus europaeus*, crested tit *Parus cristatus* and chiffchaff *Phylloscopus collybita* typically occurred in pine-dominated mosaics (Fig. 2).

For carabid beetle assemblages (Fig. 3), the first ordination axis showed a landscape structure and composition gradient from less fragmented mosaics dominated by open habitats (firebreaks = −0.85) to more fragmented mosaics dominated by wooded habitats (edge density = 0.44, mature pines = 0.39), along the north–south geographical gradient
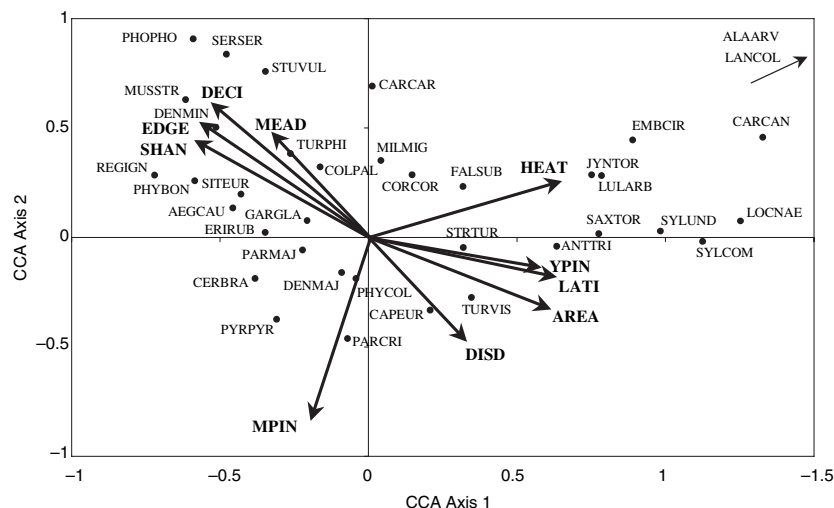

Figure 2 CCA ordination biplot of bird assemblages and landscape attributes. Abbreviations of species names as in Table 1. Additional species are: AEGCAU, *Aegithalos caudatus*; CAPEUR, *Caprimulgus europaeus*; CARCAR, *Carduelis carduelis*; CERBRA, *Certhia brachydactyla*; FALSUB, *Falco subbuteo*; JYNTOR, *Jynx torquilla*; LULARB, *Lullula arborea*; MILMIG, *Milvus migrans*; PARMAJ, *Parus major*; PHYBON, *Phylloscopus bonelli*; PYRPYR, *Pyrrhula pyrrhula*; REGIGN, *Regulus ignicapillus*. Abbreviations of landscape attributes are: AREA, mean patch area; DECI, deciduous wood cover; DISD, distance to the nearest deciduous wood; EDGE, edge density; FIRE, firebreak cover; HEAT, heathland cover; LATI, latitude; MEAD, meadow cover; MPIN, mature pine cover; SHAN, Shannon index; YPIN, young pine cover.

Figure 3 CCA ordination biplot of carabid assemblages and landscape attributes. See Fig. 2 for abbreviations of attributes and Table 2 for species abbreviations. Additional species are: AMALUN, *Amara lunicollis*; BADMER, *Badister meridionalis*; BEMDOR, *Bembidion doris*; CALCIN, *Calathus cinctus*; CALERR, *Calathus erratus*; CALFUS, *Calathus fuscipes*; CALMEL, *Calathus melanocephalus*; DYSGLO, *Dyschirius globosus*; LEIFUL, *Leistus fulvibarbis*; LEISPI, *Leistus spinibarbis*; NEBBRE, *Nebria brevicollis*; NEBSAL, *Nebria salina*; NOTQUA, *Notiophilus quadripunctatus*; PLAOBS, *Platynus obscurus*; PLARUF, *Platyderus ruficollis*; POEVER, *Poecilus versicolor*; PSERUF, *Pseudophonus rufipes*; SYNFOV, *Syntomus foveatus*.
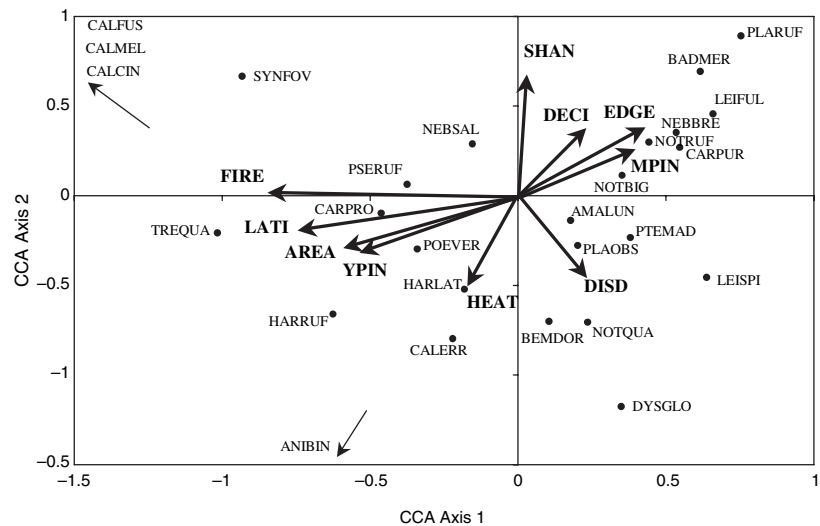
(latitude = −0.76). The second axis was related to increasing landscape heterogeneity (Shannon index = 0.66) from homogeneous mosaics dominated by heathlands (−0.53) and distant from the nearest deciduous wood (−0.47). A typical carabid assemblage with *Calathus fuscipes*, *Calathus cinctus*, *Calathus melanocephalus*, *Syntomus foveatus*, *Trechus quadristriatus* and *Carabus problematicus* occurred in mosaics dominated by large firebreaks, while *Platyderus ruficollis*, *Badister meridionalis*, *Leistus fulvibarbis*, *Nebria brevicollis*, *Notiophilus rufipes* and *Carabus purpurascens* were associated with mosaics of deciduous and pine woodlands (Fig. 3). The abundance of open-habitat species such as *Anisodactylus binotatus*, *Calathus erratus*, *Harpalus rufipalpis* and *Bembidion doris* was related to the cover of heathlands and young pine plantations.

Variance partitioning for species assemblages

The decomposition of the variation explained by the three sets of explanatory variables showed that for both groups of taxa the separate effects of landscape composition, landscape structure and spatial variables were significant at $P < 0.001$ (Monte Carlo tests with 2000 permutations). For both groups of taxa, landscape composition explained the highest part of the variation: 16.0% for birds and 12.2% for carabids (Figs 4 & 5). Considering the independent effects (i.e. after removing the joint effects of two other variable sets), landscape composition still explained more variation than landscape structure and spatial variables (10.1%, $P < 0.001$ for birds, 5.7%, $P < 0.05$ for carabids). Independent effects of spatial variables (4.6%, $P < 0.001$) and landscape structure (3.3%, $P < 0.01$) were still significant for birds but not for carabids (Fig. 5). However, the joint effect of the three variable sets was higher than the independent effect of landscape structure for birds (Fig. 4). The joint effect of landscape composition and landscape structure, and the joint effect of spatial variables and landscape structure were very low for both taxa, whereas the joint effect of landscape composition and spatial variables represented a higher proportion of variation in the case of carabids (Fig. 5).
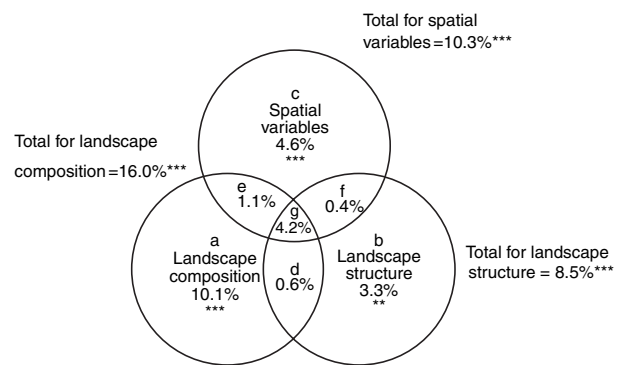

Figure 4 Variance partitioning of total variance explained by a set of partial CCA for bird assemblages. Significance levels according to Monte Carlo permutation tests with 2000 permutations: ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$, ns = non-significant. The total variance explained by the three sets of explanatory variables is 24.3%***. Letters *a*, *b*, *c* indicate the independent effects of spatial variables, landscape composition and structure; *d*, *e*, *f*, *g* indicate the joint effects.
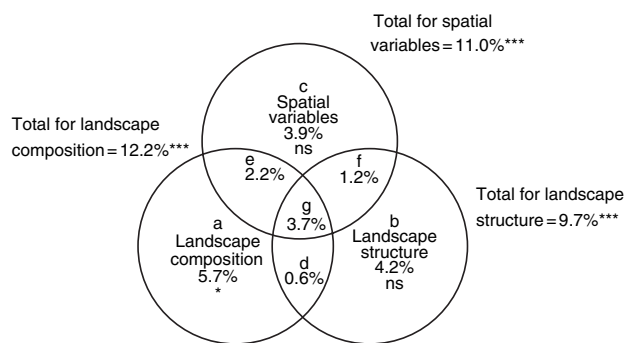

Figure 5 Variance partitioning of total variance explained by a set of partial CCA for carabid beetle assemblages. The total variance explained by the three sets of explanatory variables is 21.4%***. See caption to Fig. 4 for significance levels and letters.

Spatial patterns in species abundances

All landscape attributes showed significant spatial autocorrelation for at least one distance lag in Moran's *I* correlograms. Shannon index and cover of deciduous woods gradually decreased from the south-west to the north-east of the study area, whereas mean patch area and cover of firebreaks and young pine plantations decreased from the north-east to the south-west.

For birds, 31 species had significant correlograms at the Bonferroni-corrected level for at least one distance lag. Maps of species abundance and the shape of associated correlograms pointed out three main types in spatial distribution: (1) species showing a patchy distribution across the whole landscape (e.g. hoopoe, *Upupa epops*, Fig. 6a, melodious warbler, *Hippolais polyglotta*), (2) species showing a patchy distribution restricted to the south-western (e.g. wood pigeon, *Columba palumbus*, Bonelli's warbler) or the north-eastern parts of the landscape (e.g. skylark, grasshopper and Dartford warblers, Fig. 6b), and (3) species showing gradient distributions from the south-west (e.g. blackbird, *Turdus merula*, song thrush, *Turdus philomelos*, blue tit, *Parus caeruleus*) or the north-east (e.g. tree pipit, *Anthus trivialis*, stonechat, *Saxicola torquata*, whitethroat, *Sylvia communis*). There was no significant autocorrelation in the abundance of several forest generalists because they were randomly distributed across the whole landscape (e.g. cuckoo, *Cuculus canorus*, great spotted woodpecker, *Dendrocopos major*, great tit, *Parus major*, chaffinch, *Fringilla coelebs*).

For carabid beetles, eight species had significant Morans' *I* correlograms at the Bonferroni-corrected level for at least one distance lag. *Carabus purpurascens* (Fig. 6c), and *Notiophilus biguttatus* occurred in the whole landscape except the north-eastern part. *Carabus problematicus*, *Carabus nemoralis*, *Trechus quadristriatus*, *Anisodactylus binotatus*, *Harpalus latus* and *Harpalus rufipalpis* (Fig. 6d) were rare or absent from the south-western part of the landscape and were more abundant in the northern part.

Species abundances and landscape attributes

The abundance of 31 bird species was significantly correlated with at least one landscape attribute at the uncorrected significance level, and 23 species at the Bonferroni-corrected significance level (Table 1). The abundance of 14 forest birds was correlated with deciduous wood cover, among which three were also correlated with distance to the nearest deciduous wood (blackbird, blackcap, *Sylvia atricapilla*, and blue tit). Most forest species were also correlated with edge density (wood pigeon, great and lesser spotted woodpeckers, wren, *Troglodytes troglodytes*, robin, *Erithacus rubecula*, blackbird, song thrush, blackcap, spotted flycatcher, blue tit and jay, *Garrulus glandarius*). Four species using both deciduous woodland patches for nesting and open habitats for feeding (hoopoe, redstart, starling, *Sturnus vulgaris*, and serin, *Serinus serinus*) were also associated with the cover of meadows, which is a rather rare habitat within the study area. Ten open habitat species had significant correlations with both heathlands and young pine plantations, except the Dartford warbler which was only associated with heathlands, and the melodious warbler with young pine plantations (Table 1). These open habitat specialists were also correlated with mean patch area, except for stonechat and melodious warbler. Firebreak cover was correlated with the abundance of six species nesting in woodlands or their edges, and feeding in grasslands: turtle dove, *Streptopelia turtur*, tree pipit, mistle thrush, red-backed shrike, carrion crow, *Corvus corone*, and cirl bunting (Table 1).

For carabid beetles, the abundance of 10 species was significantly correlated with at least one landscape attribute at the uncorrected significance level, and seven species at the Bonferroni-corrected significance level (Table 2). Three woodland carabids (*C. purpurascens*, *N. rufipes*, *N. biguttatus*) were significantly correlated with edge density but not with deciduous wood cover or with distance to nearest deciduous wood. *Pterostichus madidus* was the only forest species that was significantly correlated with both deciduous wood cover and edge density. In addition, *N. rufipes* was correlated with the cover of meadows and *N. biguttatus* with Shannon index and mature pine cover. Six carabids of open habitat (*C. problematicus*, *C. nemoralis*, *T. quadristriatus*, *A. binotatus*, *H. latus* and *H. rufipalpis*) were correlated with mean patch area and/or the cover of heathlands, firebreaks and young pine plantations (Table 2).

DISCUSSION

The use of grid sampling on the same locations for two groups of taxa is an accurate method of testing for spatial structure in species distribution patterns and for understanding how these are shaped by landscape composition and structure. Moreover, the interest in comparing two groups of taxa is to examine whether similar trends exist among species with similar ecological preferences or life-history traits, irrespective of their phylogeny (Mac Nally *et al.*, 2004).

The spatial distribution patterns of carabid beetles have been investigated at regional (Dufrêne, 1992; Eyre *et al.*, 2005) or microhabitat scales (Niemelä *et al.*, 1992; Thomas *et al.*, 2001), but less commonly at the landscape scale (Aviron *et al.*, 2005). Bird communities have been studied more extensively at the landscape scale, but mesoscale studies on a large continuous area using grid-based sampling are rare both for birds (Balent & Courtiade, 1992; Heikkinen *et al.*, 2004; Titeux *et al.*, 2004) and carabids (Judas *et al.*, 2002; Holland *et al.*, 2005). Our results suggest that spatial distribution patterns of bird and carabid species at a mesoscale of 400×400 m were mainly determined by landscape composition (habitat cover) rather than landscape structure or true spatial dependence. Canonical partitioning showed that 42% of the total explained variation for the ordination of bird assemblages was due to the independent effect of landscape composition, whereas the pure effects of spatial variables and landscape structure explained 19% and 14% of this total variation, respectively. For carabid beetles, 27% of the explained variation was due to
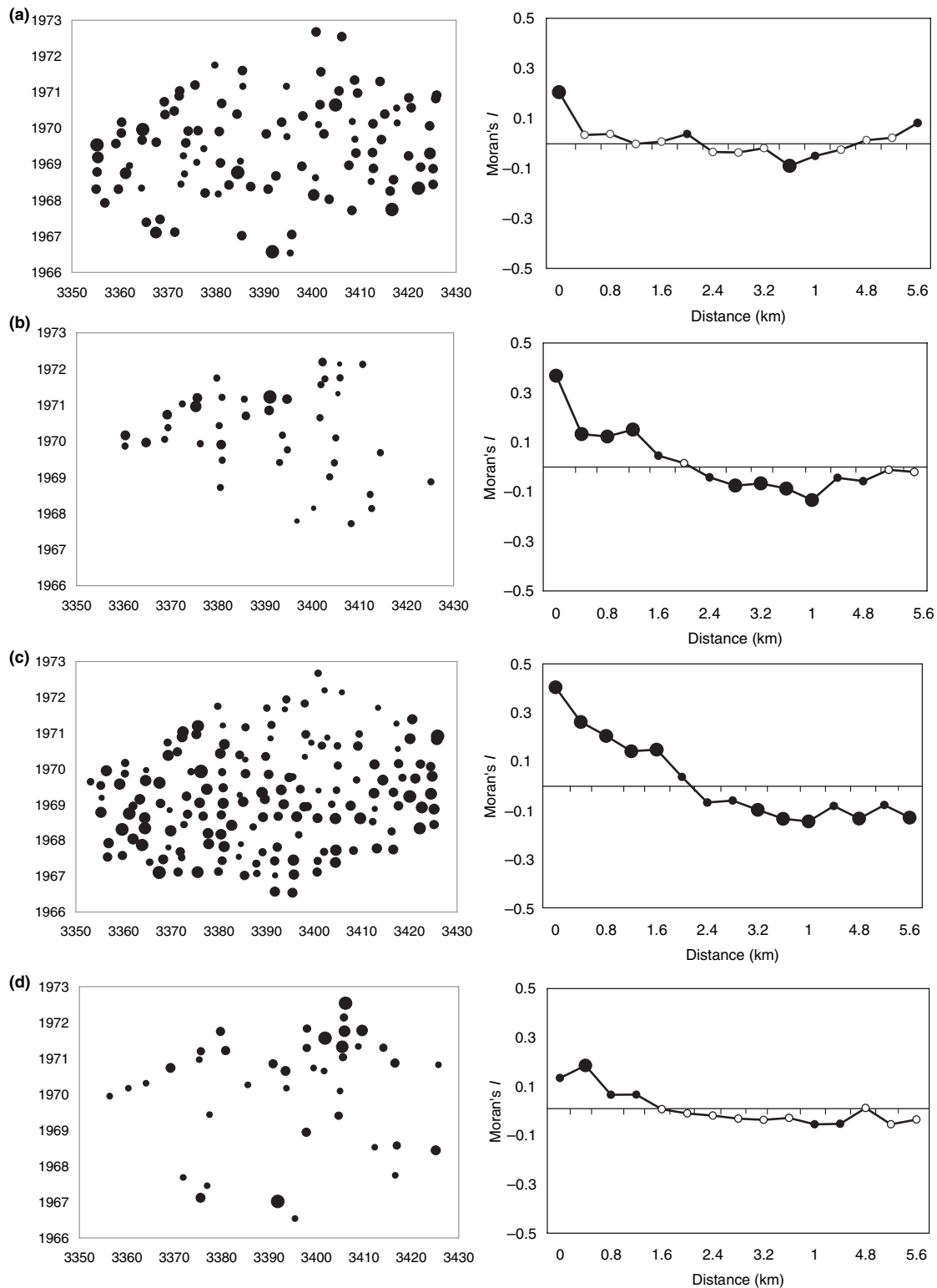
Figure 6 Examples of abundance maps (geographical coordinates in the Lambert II extended grid system) and Moran's *I* correlograms for selected species of breeding birds: (a) hoopoe, *Upupa epops*, (b) Dartford warbler, *Sylvia undata*; and carabid beetles: (c) *Carabus purpurascens* and (d) *Harpalus rufipalpis*. On the maps, black dots are proportional to the abundance index ranging from 0.5 to 5 for birds and to the log-transformed number of caught individuals for carabids. The correlograms give Moran's *I* coefficient for 15 equidistant lags of 400 m. Large black dots indicate a Bonferroni-corrected significance level of *P* < 0.0033, small black dots indicate a significance level of *P* < 0.05 and small white dots indicate non-significant values, according to a Monte Carlo test with 1000 permutations.

Table 1 Mantel correlation coefficients between Euclidean distances of bird species abundance and landscape attributes

Species	Abbreviation	AREA	SHAN	EDGE	DISD	MEAD	FIRE	HEAT	YPIN	MPIN	DECI
Columba palumbus	COLPAL	0.013	0.008	0.100*	0.034	0.032	−0.003	−0.060	0.004	−0.040	0.117*
Streptopelia turtur	STRTUR	−0.036	−0.025	−0.050	0.024	−0.091	0.154*	−0.041	0.031	−0.008	−0.037
Upupa epops	UPUEPO	−0.039	−0.015	−0.030	−0.019	0.086*	−0.021	−0.026	−0.016	−0.002	0.001
Dendrocopos major	DENMAJ	0.011	0.015	0.083***	0.013	0.062	−0.020	−0.017	0.066	0.044	−0.019
Dendrocopos minor	DENMIN	−0.046	0.121**	0.096**	0.015	0.066	−0.006	−0.075	−0.063	0.017	0.166**
Alauda arvensis	ALAARV	0.113*	0.120**	0.007	−0.056	−0.078	0.195***	0.543***	0.185**	0.158***	−0.071
Anthus trivialis	ANTTRI	0.091**	0.051*	0.066***	0.006	−0.026	0.073*	0.229***	0.099***	0.019	0.039
Troglodytes troglodytes	TROTRO	0.056	0.043	0.053*	0.007	0.033	0.030	0.040	0.120***	0.091***	0.024
Erithacus rubecula	ERIRUB	0.048	0.054*	0.087***	0.015	0.062	−0.033	−0.028	−0.018	0.035	0.228***
Phoenicurus phoenicurus	PHOPHO	−0.046	−0.006	0.010	0.005	0.224*	−0.046	−0.067	−0.040	0.022	0.118*
Saxicola torquata	SAXTOR	0.025	0.036	0.001	−0.008	−0.076	−0.038	0.259***	0.106*	0.010	−0.036
Turdus merula	TURMER	0.073*	0.143***	0.208***	0.084*	0.161*	0.030	−0.041	0.008	0.060*	0.219***
Turdus philomelos	TURPHI	0.018	0.039	0.140***	0.042	0.043	−0.061	−0.070	−0.015	0.065*	0.304***
Turdus viscivorus	TURVIS	0.032	0.059	−0.013	−0.032	−0.090	0.153**	0.135*	−0.051	0.015	−0.075
Sylvia atricapilla	SYLATR	0.160***	0.154***	0.171***	0.087***	−0.018	0.028	0.091*	0.056	0.016	0.199***
Sylvia communis	SYLCOM	0.147***	0.089*	0.029	0.087*	−0.097	−0.014	0.211***	0.322***	0.043	−0.077
Sylvia undata	SYLUND	0.112*	−0.007	−0.007	−0.021	−0.095	−0.024	0.263***	0.076	−0.002	−0.095
Locustella naevia	LOCNAE	0.178***	0.095*	0.045	0.042	−0.087	0.016	0.257***	0.228***	0.037	−0.064
Hippolais polyglotta	HIPPOL	0.002	−0.012	−0.027	0.089**	−0.063	−0.043	−0.056	0.148***	−0.043	−0.051
Phylloscopus collybita	PHYCOL	0.025	0.016	0.029	−0.018	0.103*	0.007	0.103**	0.052	0.129***	0.063*
Muscicapa striata	MUSSTR	−0.004	0.023	0.093*	0.003	0.035	−0.030	0.001	−0.051	−0.042	0.235***
Parus caeruleus	PARCAE	0.054	0.101***	0.136***	0.112***	0.116*	−0.027	−0.049	−0.019	0.038	0.333***
Parus cristatus	PARCRI	0.002	0.049	0.053	−0.001	−0.027	−0.037	−0.041	−0.040	0.116***	−0.041
Sitta europaea	SITEUR	−0.042	0.044	0.042	0.042	0.112*	−0.057	−0.069	−0.059	−0.041	0.246***
Lanius collurio	LANCOL	0.234***	0.163***	0.052	0.028	0.010	0.251***	0.292***	0.207***	0.104*	−0.071
Corvus corone	CORCOR	0.004	0.020	0.015	0.001	0.100**	0.056*	0.021	0.038	0.048*	0.016
Garrulus glandarius	GARGLA	0.022	0.039	0.066***	0.020	0.045	−0.038	−0.041	−0.011	−0.010	0.086*
Sturnus vulgaris	STUVUL	−0.020	0.016	0.066*	−0.012	0.276***	0.089	−0.067	−0.028	0.066	0.110*
Carduelis cannabina	CARCAN	0.108*	0.069	0.008	−0.057	−0.086	0.076	0.191**	0.296***	0.172***	−0.072
Serinus serinus	SERSER	−0.034	−0.003	0.053	0.042	0.206*	−0.055	−0.045	−0.031	0.001	0.122*
Emberiza cirlus	EMBCIR	0.113*	0.027	−0.015	0.018	−0.031	0.230***	0.127*	0.116*	0.054	−0.088

Significance level according to a Monte Carlo test with 1000 permutations: ***$P < 0.005$ (Bonferroni-corrected), **$P < 0.01$ and *$P < 0.05$. See Fig. 2 for the abbreviations of landscape attributes

Table 2 Mantel correlation coefficients between Euclidean distances of log-transformed abundance of carabid beetles and landscape attributes

Species	Abbrev.	AREA	SHAN	EDGE	MEAD	FIREB	HEAT	YPINE	MPINE	DECID
Carabus purpurascens	CARPUR	0.064*	0.015	0.033*	0.042	0.106***	0.034	0.077**	0.027	−0.009
Carabus problematicus	CARPRO	0.117*	0.025	−0.026	−0.106	0.231***	0.111*	0.032	0.028	−0.097
Carabus nemoralis	CARNEM	0.060	0.020	−0.045	−0.062	0.235***	0.236***	−0.037	−0.042	−0.089
Notiophilus rufipes	NOTRUF	0.004	0.014	0.096**	0.180**	−0.062	−0.069	−0.005	−0.014	0.094
Notiophilus biguttatus	NOTBIG	0.101*	0.073*	0.089**	0.092	−0.065	−0.080	−0.016	0.079*	0.025
Trechus quadristriatus	TREQUA	0.111*	0.077	−0.001	−0.034	0.301***	0.225**	0.011	0.043	−0.004
Pterostichus madidus	PTEMAD	0.016	0.073	0.108**	0.087	−0.039	0.106*	−0.033	−0.020	0.137**
Anisodactylus binotatus	ANIBIN	0.168*	0.178***	0.052	−0.070	0.066	0.303***	0.223***	0.142***	−0.048
Harpalus latus	HARLAT	0.155**	0.067	0.009	−0.050	0.059	−0.026	0.155***	0.060	−0.103
Harpalus rufipalpis	HARRUF	0.123*	0.092*	−0.008	−0.069	0.124*	0.291***	0.134***	0.116**	−0.085

Significance level according to a Monte Carlo test with 1000 permutations: ***$P < 0.005$ (Bonferroni-corrected), **$P < 0.01$ and *$P < 0.05$. See Fig. 2 for the abbreviations of landscape attributes. DISDEC had no significant values.

the independent effect of landscape composition, which had the only pure significant effect among the three variable sets.

Several authors have demonstrated that, for birds at the landscape scale, a major part of spatial structure can be explained by environmental variation (Hobson *et al.*, 2000; Lindenmayer *et al.*, 2002; Titeux *et al.*, 2004). Moreover, the effect of habitat cover is generally more important than the effect of landscape configuration or structure (Trzcinski *et al.*, 1999; Drapeau *et al.*, 2000; Cushman & McGarigal, 2002). At mesoscales, bird abundance is not related to landscape heterogeneity as such but depends more on the distribution patterns of important habitats, so that most of the spatial structure in bird abundance patterns can be explained by the clumping of preferred or avoided habitats (Virkkala *et al.*, 2004). When there is a significant independent spatial effect, it can be caused by an unmeasured factor such as habitat quality, interspecific competition for food or aggregated distributions of individual breeders (Wiens, 1994; Fuller *et al.*, 2004).

For carabid beetles, Judas *et al.* (2002) argued that micro-climatic habitat associations scale up to mesoscale distributions within a landscape. Here, we found evidence that landscape composition had the only pure significant effect on the ordination of carabid beetles at the landscape scale. However, as a large part of variation in carabid beetle assemblages remained unexplained, other factors involved in carabid species' distribution at finer scales may also have an important role at the mesoscale. These factors include microclimate, vegetation structure, prey density, predation, competition or localized oviposition sites (Niemelä *et al.*, 1992; Antvogel & Bonn, 2001; Thomas *et al.*, 2001; Magura, 2002; Brose, 2003).

Spatial heterogeneity and landscape matrix composition

Mesoscale spatial heterogeneity was an important factor for the ordination of bird and carabid beetle assemblages in this mosaic landscape dominated by pine plantations. Spatial heterogeneity or habitat diversity at the landscape level generally increases species richness of arthropods (Duelli & Obrist, 2003; Weibull *et al.*, 2003) and birds (Balent & Courtiade, 1992; Titeux *et al.*, 2004). However, species responses to spatial heterogeneity depend on the spatial scale at which heterogeneity is measured and on contrasting life history traits among species, such as home range sizes or food requirements (Wiens, 1994; Mac Nally *et al.*, 2004; Tews *et al.*, 2004; Aviron *et al.*, 2005). Our results do not support the hypothesis that most species abundances are positively associated with spatial heterogeneity in the surrounding matrix. Thus, we argue that mesoscale spatial heterogeneity is not a direct factor explaining species distributions in complex landscapes but a surrogate for the occurrence of particular habitats. As pointed out by Heikkinen *et al.* (2004), this could be because habitat diversity indices and other landscape metrics do not take into account habitat quality.

By contrast, landscape composition was the main factor for the ordination of both bird and carabid assemblages in the study area. One striking result was the importance of the amount of open habitats, especially heathlands, young pine plantations and firebreaks for both carabids and birds, although the whole landscape mosaic was largely dominated by forests. The other important habitat type was the cover of deciduous woods, especially for woodland birds. Landscape matrix composition is now considered to be a major factor explaining species occurrence within habitat patches (Wiens, 1994; Norton *et al.*, 2000; Dauber *et al.*, 2003; Watson *et al.*, 2005), in contradiction with the island biogeography theory, where the area effect was considered to be predominant (Haila, 2002; Kupfer *et al.*, 2006). However, this influence is often related to the occurrence of particular habitats, and especially semi-natural vegetation (Berg, 2002; Duelli & Obrist, 2003; Fuller *et al.*, 2004; Purtauf *et al.*, 2005).

The habitat composition of the surrounding matrix may influence patch habitat quality (Sisk *et al.*, 1997; Desender *et al.*, 1999), especially the proximity to other habitats used as foraging areas (Estades & Temple, 1999; Saab, 1999). Our results suggest that some bird species used complex mosaics of habitats, because they generally bred in woodlands and foraged in adjacent grasslands, along road verges or firebreaks. Such species included turtle dove, hoopoe, mistle thrush, red-backed shrike, starling or cirl bunting, most of them having important conservation value (Virkkala *et al.*, 2004). These species supported the habitat complementation hypothesis, which predicts a need for non-substitutable resources found in two different adjacent habitats within a landscape mosaic (Dunning *et al.*, 1992).

Fragmentation effects on woodland and open habitat species

The amount of native deciduous trees at both stand scale and landscape scale is a determining factor for the dynamics of species assemblages in conifer-dominated landscapes (Estades & Temple, 1999; Hobson *et al.*, 2000; Norton *et al.*, 2000; Lindenmayer *et al.*, 2002). A geographical gradient from potential source forests can drive the spatial distribution of species within a landscape (Magura, 2002; Miller *et al.*, 2004). We found such a spatial gradient with increasing abundance towards large deciduous woods of the western part of the landscape for many woodland birds, but such patterns were less obvious for woodland carabids, that are poor dispersers compared to birds. In addition, some bird species were restricted to oak and mixed oak–pine fragments within the study area (lesser spotted woodpecker, Bonelli's warbler, spotted flycatcher and long-tailed tit, *Aegithalos caudatus*). The abundance of some woodland birds significantly decreased with increasing distance from large deciduous forests (e.g. blackbird, blackcap and blue tit), indicating an overall negative effect of oak woodland fragmentation. The use of fragmentation variables calculated for specific habitats rather than for the whole landscape mosaic, irrespective of habitat, could have

helped detect supplementary negative effects of forest fragmentation in the study area.

However, fragmentation can also become a positive phenomenon, for example when food is taken outside the main breeding habitat (Dunning *et al.*, 1992; Estades & Temple, 1999). For carabid beetles, edge effects between forests and clearcuts do not affect forest specialists (Heliölä *et al.*, 2001) and increase species richness (Magura, 2002), but large-scale woodland fragmentation by agriculture negatively affects large forest species with low mobility (Desender *et al.*, 1999; Aviron *et al.*, 2005). Several authors have demonstrated that forest fragmentation can favour woodland birds because of positive edge effects (Sisk *et al.*, 1997; Berg, 2002; Herrando & Brotons, 2002) or habitat compensation between patches (Norton *et al.*, 2000; Lindenmayer *et al.*, 2002). Some species may compensate for a loss of their preferred habitat by shifting to less preferred habitat types such as coniferous plantations, but these plantations may act as population sinks and ecological traps if they suffer lower reproductive success or higher mortality (Norton *et al.*, 2000). However, regarding the relatively recent history of pine plantations in the study area, we assumed that time-lags and regional population dynamics acting at larger spatial and temporal scales may enhance or mitigate species responses to forest fragmentation.

Birds and carabid beetles that are specialists of open habitats were largely restricted to the largest patches of heathlands, young pine plantations and firebreaks of the north-eastern part of the landscape. As a result, species composition changed and species diversity increased when moderately large open habitats allowed early-successional specialists to penetrate into the wooded matrix of pine plantations. Such a colonization of open habitats within mosaic forests composed of different successional stages by early-successional species has been documented in boreal, temperate and Mediterranean forests for birds and carabid beetles (Gjerde & Saetersdal, 1997; Desender *et al.*, 1999; Drapeau *et al.*, 2000; Heliölä *et al.*, 2001; Brotons *et al.*, 2005). Cushman & McGarigal (2003) demonstrated that early-successional species were lost when mature forest covered more than 80% of the landscape, whereas mature forest species were still present in landscapes where mature forest was rare or absent.

In the present study, most birds and carabids of open habitats had a patchy or aggregated distribution and high habitat specialization. Such species of conservation concern included woodlark, *Lullula arborea*, tawny pipit, *Anthus campestris*, Dartford warbler or red-backed shrike for birds; *Poecilus kugelanni*, *Calathus erratus*, *Calathus cinctus* or *Harpalus neglectus* for carabids. We argue that it is important to maintain open habitats at a moderate level within maritime pine plantation forests for the long-term conservation of early-successional species, which are probably relicts of the past open landscape (Barbaro *et al.*, 2005). The maintenance of suitable open habitats within a forest matrix may enhance colonization by open-habitat species after a strong disturbance such as clearcutting (Brotons *et al.*, 2005). As movement between habitat patches is the key process determining how the distribution of patches affects populations (Wiens, 1994), further research is needed on the mechanisms involved in the use of multiple habitats by species in mosaic landscapes, and on the importance of particular habitat combinations at the landscape scale for the conservation of biodiversity.

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