



Spatial extent of bird species response to landscape changes: colonisation/extinction dynamics at the community-level in two contrasting habitats

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Animal community dynamics in changing landscapes are primarily driven by changes in vegetation structure and ultimately by how species respond to these changes and at which spatial scale. We consider two major components of local community dynamics, species colonisation and extinction. We hypothesise that 1) the optimal spatial extent needed to accurately predict them will differ between these two processes; 2) it will also likely differ from species to species as a result of life history traits differences related to differences in habitat selection and 3) that a species' primary habitat will determine the spatial extent at which it perceives change in vegetation structure. We used data collected over 25 yr in a changing Mediterranean landscape to study bird species local colonisation and extinction patterns in two groups of species typical from two habitats: open farmland and woodland. Vegetation changes were measured at spatial extents ranging from 0.2 to 79 ha. Local species colonisation and extinction estimates were computed using a method accounting for heterogeneity in detection probability among species. We built linear models between local species colonisation/extinction estimates and vegetation changes and examined variations in model quality with respect to the spatial extent at which vegetation changes had been measured. Models for open habitat species showed that colonisation processes operated at the landscape scale (79 ha), while extinction was more tightly linked to local habitat requirements (0.2 ha). Models for woodland species presented a low and constant model quality whatever the spatial extent considered. Our results suggest that the dynamics of the woodland species considered responded to a combination of vegetation changes at several scales and, in particular, to changes in the vertical structure of the vegetation. We highlight the need to explicitly consider spatial extent in studies of habitat selection and of habitat and population dynamics to improve our understanding of the biological consequences of land use changes and guide more effective conservation efforts.

In a context of large-scale environmental changes, ecology aims at understanding the scaling of the responses of species and communities to temporal and spatial changes in habitat structure and composition (Bossenbroek et al. 2005). At the landscape level (Mayer and Cameron 2003), local processes in community dynamics are driven by temporal changes in the extent and spatial distribution of suitable habitats, either patch size or habitat quality (Franken and Hik 2004). With the recognition of the importance of spatial heterogeneity in the past two decades, ecology has increasingly focused on the spatial dimension of ecological patterns and processes (Turner et al. 2001, Wu and Hobbs 2002). Landscapes are known to be hierarchically structured and vegetation patterns are affected by the choice of grain (resolution of a map) or extent (spatial area considered to measure patterns) (Wu 2004). The ability to predict local animal

species dynamics in response to habitat changes is likely to be affected by the spatial extent at which we measure temporal vegetation changes as well as by individual species characteristics. Mayer and Cameron (2003) emphasized the need to use several scales to properly address these issues.

Two main processes determine the response of an animal species to landscape changes: local colonisation and local extinction. Local colonisation is understood as the presence of a species in a location from which it was absent in earlier censuses, whereas local extinction is understood as the missing of a species from a location where it was present in earlier censuses (Nichols et al. 1998). We hypothesise that the spatial extent best suited to accurately predict local colonisation and extinction could differ between these two processes. Indeed, as an animal species can temporarily persist (i.e. have a low local extinction rate) because of site

fidelity (Matthiopoulos et al. 2005), even after severe habitat fragmentation (Hanski et al. 1995) or after a sharp decrease in habitat quality (Eriksson 1996), local extinction could be more closely tied to the local scale than to the landscape scale. On the other hand, as local colonisation can be delayed or facilitated by processes operating at larger spatial scales (Brotons et al. 2005) (e.g. presence of a source of immigrants) and because species often use habitat cues at multiple spatial scales to select a new habitat (Fahrig and Merriam 1985) we expected that local colonisation is likely to be explained by changes in vegetation occurring at a larger spatial scale than for local extinction. The need to consider different scales has been emphasized by several studies. Pearman (2002), for instance, found that different tropical forest bird species guilds differed in the scale at which their species richness related to their environment. Robinson et al. (2004) showed that differences in the scale at which farmland birds responded to habitat were related to the extent of their between-season movements. One can therefore speculate that the spatial extent at which local extinction and colonisation will occur is likely to differ with species life-history traits such as habitat range, migratory status, social behaviour, food regime or territory size. These traits are all involved in the process of habitat selection (Stearns 1977), which is often approached by the analysis of patterns in habitat use (Jones 2001). Therefore, we hypothesised that differences in habitat use between species could, at least in part, explain the spatial extent at which species differ in their response to vegetation change. For example, species using closed habitats could be likely to respond to changes in conditions at the local scale because of the high structural complexity of their habitat. Species using open habitats could be more influenced by changes at a larger scale. Such differences among species in the spatial extent of their response to vegetation change would, in turn, suggest differences in the mechanisms that influence habitat selection.

To test these hypotheses we analysed bird community dynamics in a context of land abandonment in a Mediterranean region. In the traditionally heterogeneous Mediterranean landscapes, land abandonment results in a decrease of open habitats and an increase of woodlands, and triggers decreases/increases of bird species associated with open habitats/woodlands (Sirami et al. 2007). Bird species associated with these two extremes of the vegetation gradient provided a framework to study how vegetation changes at different spatial scales predicted the likelihood of species local colonisation or extinction in these two contrasting species groups (open habitats and woodlands).

Material and methods

Study area

The study area was situated 20 km north of Montpellier (southern France) (43°47'N, 03°50'E). It covers 2800 ha and includes a karstic limestone plateau, marly hills and plains, and cliffs. Altitude ranges from 125 to 658 m at the Pic Saint Loup. The climate is Mediterranean, with moist and cool winters. The annual average rainfall ranges from 950 to 1350 mm, average maximum temperature during

the warmest month is 28°C and average minimum temperature during the coldest month is -1°C (Debussche and Escarre 1983).

The study area is a typical Mediterranean mosaic of grasslands and croplands embedded within a matrix of shrublands and woodlands (Preiss et al. 1997). Grasslands were maintained by extensive sheep grazing until the middle of the 20th century. Shrublands were also used for grazing sheep and for the production of juniper oil. The oak woodlands were coppiced at 30-yr intervals for charcoal until the last peak of intensive use during the World War II (Debussche et al. 1987). Around the 1960s, a period of rapid land abandonment started with a strong decrease in sheep grazing and the abandonment of oak coppicing. As a result, significant vegetation changes occurred in the study area during the study period (1978–2003): open habitats (grasslands and shrublands) declined dramatically while woodlands increased (Sirami et al. 2007). Consequently, there was an overall shift of the bird community in favour of woodland species (Sirami et al. 2007). Of seven species dependent on open habitats, the occurrence rate of five decreased significantly whereas it increased for two species. The occurrence rate increased significantly for seven species relying on closed woodlands, while it decreased only for two woodland species (Sirami et al. 2007).

Bird community sampling

We used bird data from the long-term monitoring program described by Sirami et al. (2007). The bird community was surveyed at 194 census-plots defined in 1978 by Preiss et al. (1997) with a minimum distance of 250 m between plots (Fig. 1). At each plot, birds were counted once in each of the three study years. We used a randomized order in 1978, and followed the same order in 1992 and 2003 so as to be consistent in the timing of the bird community sampling among the three periods. Birds were counted by means of 20 min point counts with unlimited distance (Bibby et al. 1992) by J. L. Martin in 1978, E. Preiss in 1992 and C. Sirami in 2003. We excluded from the analysis all species that were recorded only in 5 plots or less, as their presence was likely to be the result of stochastic factors or of the presence of highly specific habitat features not relevant to the present study. As a result, we were left with 34 species that had all been recorded in more than ten plots within one year.

In order to assess long-term species dynamics, we focused on changes between 1978 and 2003. Species occurrences can vary significantly from one year to the next, which can bias estimations of long-term trends. But the strong relationship between species long-term trends obtained from 1978–1992 (Preiss et al. 1997) and those obtained from 1978–2003 (linear model between indexes of abundance change 1978–2003 and 1992–2003; Sirami et al. 2007) suggested that inter-annual variation did not bias estimations of long-term trends. To confirm this assumption, we re-sampled bird communities in 2004 and 2005 for 50 of the 194 census points sampled in 1978 and 2003 (unpubl.). The use of any of the consecutive years (2003, 2004 or 2005) yielded to similar long-term trends for all species when compared with the 1978 data of

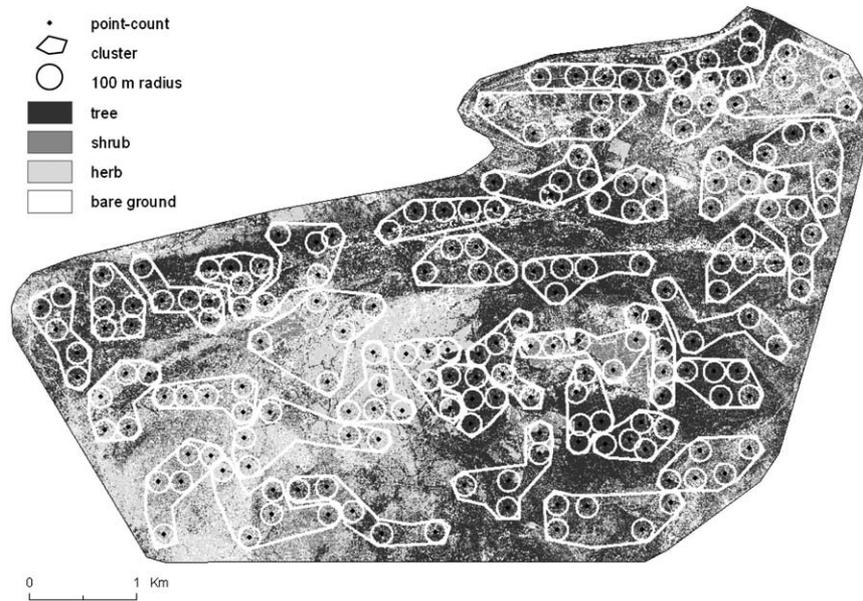


Figure 1. Map of the study area with the location of the 194 point-counts and a 100 m radius around each census-point, the 39 clusters and the vegetation map in 1981.

the same 50 points. We therefore considered that in our data set, inter-annual variation had little effect on the long-term species dynamics we were investigating.

Identification of open habitat and woodland species

As species life-history traits, in particular habitat selection, can vary significantly through a species' range, we used local data rather than habitat description from the literature in order to classify species as open habitat or woodland species. To do so we used the co-inertia ordination published in Sirami et al. (2007) to rank the 34 bird species along a vegetation gradient going from open habitats (grasslands with a varying amount of shrubs and/or small trees) to woodlands dominated by small trees (Fig. 2). We grouped the bird species in three classes along this gradient: species from open habitats, species from habitats dominated by shrubs and species associated with woodlands. We only

considered the species from the two extremities of this gradient because species associated with the transitory middle of the gradient ("shrubland species") were likely to have non linear responses to landscape changes (Prodon and Lebreton 1981) while species associated with the extremities of the gradient were likely to have linear responses to vegetation changes. We excluded the magpie *Pica pica* because it was linked to human modified habitats and the blue rock thrush *Monticola solitarius* because it was associated with rocky outcrops and clearings within woodlands. As a result, each of the two species groups had a total of 13 species (Table 1).

Vegetation classification

To assess temporal changes in the vegetation we used the vegetation maps obtained from a pixel classification of the 1981 and 2002 aerial photographs used by Sirami et al.

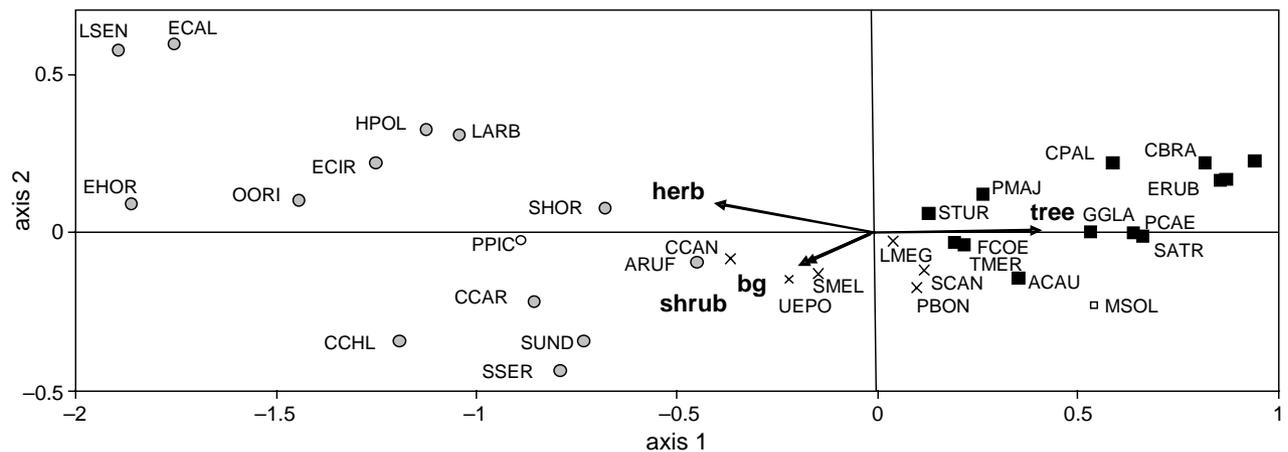


Figure 2. Co-inertia plot published in Sirami et al. (2007) with species groups: ○ open habitat species; ■ woodland species; ○/□ open habitat/woodland species excluded (see Methods) and × shrubland species (for species acronyms see Table 1; bg = bare ground).

Table 1. List of species from open habitat and woodland and their acronym (ranked according to increasing scores on axis 1 of the co-inertia analysis in Sirami et al. (2007) presented in Fig. 2; (the note 'excl.' corresponds to the two species excluded from the analyses for reasons explained in the method section).

Open habitat species	Woodland species	Shrubland species
<i>Emberiza hortulana</i> EHOR	<i>Streptopelia turtur</i> STUR	<i>Cuculus canorus</i> CCAN
<i>Lanius senator</i> LSEN	<i>Fringilla coelebs</i> FCOE	<i>Upupa epops</i> UEPO
<i>Emberiza calandra</i> ECAL	<i>Turdus merula</i> TMER	<i>Sylvia melanocephala</i> SMEL
<i>Oriolus oriolus</i> OORI	<i>Parus major</i> PMAJ	<i>Luscinia megarhynchos</i> LMEG
<i>Emberiza cirlus</i> ECIR	<i>Aegithalos caudatus</i> ACAU	<i>Phylloscopus bonelli</i> PBON
<i>Carduelis chloris</i> CCHL	<i>Columba palumbus</i> CPAL	<i>Sylvia cantillans</i> SCAN
<i>Hippolais polyglotta</i> HPOL	<i>Garrulus glandarius</i> GGGLA	
<i>Lullula arborea</i> LARB	<i>Sylvia atricapilla</i> SATR	
<i>Carduelis carduelis</i> CCAR	<i>Parus caeruleus</i> PCAE	
<i>Serinus serinus</i> SSER	<i>Certhia brachydactyla</i> CBRA	
<i>Sylvia undata</i> SUND	<i>Erithacus rubecula</i> ERUB	
<i>Sylvia hortensis</i> SHOR	<i>Regulus ignicapillus</i> RIGN	
<i>Alectoris rufa</i> ARUF	<i>Phylloscopus collybita</i> PCOL	
<i>Pica pica</i> PPIC (excl.)	<i>Monticola solitarius</i> MSOL (excl.)	

(2007). These maps identify four pixel classes: Bare Ground (little or no vegetation), Herb (herbaceous vegetation), Shrub (woody vegetation 0.5–2.5 m) and Tree (woody vegetation > 3 m). We used the cover percentage of tree, shrub, herb and bare ground as well as the Shannon diversity index [$SHDI = -\sum_{i=1}^m (P_i \ln P_i)$] with m : number of vegetation classes and P_i : proportion of area covered by vegetation type i] to describe the vegetation in each census plot in 1981 and 2002.

Spatial extent

We considered nine spatial extents to calculate vegetation changes around each census point. We choose 25 m as the most local spatial extent, an extent consistent with GPS and geo-referencing accuracy (around 10 m for each), and 500 m for the largest spatial extent. We calculated the five descriptive variables (cover of tree, shrub, herb, bare ground and vegetation diversity index) for radii of 25, 50, 75, 100, 150, 200, 300, 400 and 500 m (equivalent to 0.2, 1, 2, 3, 7, 13, 28, 50 and 79 ha; see Fig. 1 for illustration of the 100 m radius). For each census point and each radius, we obtained five predictor variables corresponding to the change between 1981 and 2002 (value 2002 minus value 1981) for each one of the five descriptive variables.

Spatial unit of analyses: the cluster

The statistical analyses of long-term datasets face two major problems: variations in detection probabilities among species and problems associated with spatial autocorrelation. For these two reasons, we were not able to use our dataset at the scale of the census point but we had to conduct our analyses at the scale of clusters of 5 census points considered as spatial replicates. The 5 census points had to be spatially close enough and located in similar habitats to be considered as spatial sampling replicates (mean distance between the two most distant census points within one cluster = 848 ± 226 m; Fig. 1). For each cluster, we were then able 1) to estimate the dynamics of the two bird species groups taking into account variations in species detection probabilities; and 2) to obtain spatially indepen-

dent response variables (cf. below “Parameter estimation”). As the number of species from the two bird species groups varied among the different clusters (according to vegetation), some clusters were included in the analyses of the dynamics of both open habitat and woodland species whereas other clusters were used only in the analysis of open habitat species or only in the analysis of woodland habitat species.

Parameter estimation

Gonzalo-Turpin et al. (2008) showed, using the PRESENCE software <www.mbr-pwrc.usgs.gov/software.html> (MacKenzie et al. 2002), that detectability biases caused by observer (confounded with year), wind velocity, cloud cover, date and sampling hour did not significantly affect occupancy rate estimations based on 20-min-long point counts. We therefore consider that such biases should have negligible effects on our estimates of local colonisation or extinction. However, as species detection probabilities varied among conditions and habitats (Gonzalo-Turpin et al. 2008) we computed estimators of species colonisation and extinction that took into account species detection probabilities (Boulinier et al. 2001). First, we used a capture-recapture method that considered the five census points as spatial replicates in order to estimate for each cluster the probability of species detection (Nichols et al. 1998). The use of this capture-recapture approach is based on the recognition that some species are likely to be missed during sampling. This method uses the widespread jackknife estimator (presented in Burnham and Overton (1979) and implemented in COMDYN (Hines et al. 1999)). We considered species from the two groups as two closed communities, defined in Boulinier et al. (2001) as a “population” of species that is well defined and not changing within a short time interval considered and within the limited area considered. We computed estimates for each of these two communities. We estimated local species detection probability for each of the 39 clusters, for the two groups of species (open habitat and woodland species) and for each year. Results obtained for our data set showed that the species detection probability varied both between

species groups (0.79 ± 0.02 for open habitat species and 0.81 ± 0.02 for woodland species) and among clusters (detection probability was lower than 0.5 in 20 of the 39 clusters at least in one year or in one species group). However, as Boulinier et al. (1998) considered that the jackknife estimator performed poorly when local species richness was low, therefore, we decided to exclude clusters for which species richness was <5 in 1978 or in 2003 (conservative threshold following Doherty et al. 2003). We should thus bear in mind that the present study may exclude clusters with high values for colonisation and extinction parameters and lead to conservative estimates of relationships between community dynamics and landscape. Nineteen of the 39 clusters were selected for the analysis on open habitat species and 27 for the analysis on woodland species. Finally, we computed parameters of colonisation and extinction that took into account this heterogeneity in species detection probability by using the procedure implemented in COMDYN. We defined estimated species colonisation as the expected number of species present in a cluster in 2003 that were absent from the same cluster in 1978 and estimated species extinction as the expected proportion of species present in a cluster in 1978 that will be absent from the same cluster in 2003 (for detailed description of estimators see Nichols et al. (1998)).

As spatial autocorrelation in the bird dataset was likely to occur at the scale of the census point (average distance 250 m), we investigated whether the clusters could be considered as spatially independent. We investigated spatial autocorrelation in the response variables by using Moran's I correlograms following Lichstein et al. (2002) and we did not identify any significant spatial autocorrelation in the response variables we studied (colonisation and extinction for the two groups).

The variables of vegetation change that were associated with the clusters were the averages over the 5 census points of the five predictor variables (average of the change in the cover percentage of tree, shrub, herb, bare ground and average change of the vegetation diversity index). We used these 5 variables as predictor variables for each of the 9 spatial extents (25–500 m).

Analyses

Vegetation changes

We verified 1) that observed vegetation changes varied with the spatial extent considered and 2) that overall vegetation changes followed similar patterns in relation to spatial extent in each set of clusters (open habitat and woodland). Indeed, differences in the relationship between colonisation/extinction and spatial extent among the two species groups could result from differences in patterns of vegetation changes among the two sets of clusters. For example, a lack of sensitivity of woodland species to spatial extent could result from a lack of significant effect of spatial extent on vegetation changes in the clusters with woodland species (27 clusters). We used vegetation changes at 25 m as our reference and compared them with changes at the other spatial extents. We calculated, for each predictor variable and each spatial extent, the absolute value of the difference between the value of the change observed at that spatial extent and the reference value (for example, absolute value ($\Delta\%tree50m - \Delta\%tree25m$)). In order to verify that there

is a significant difference between at least two of the nine spatial extents considered we tested the effect of spatial extent on the absolute value of the difference with Friedman ANOVA (for paired measures).

Bird response

We analysed bird species response to vegetation changes using linear regression between colonisation/extinction and changes in the vegetation. Normality of response and predictor variables was tested using Shapiro-Wilk test. We transformed the colonisation response variable using a square-root function. In a first step, we calculated univariate models for the 5 predictor variables at each spatial extent. We used the adjusted R-square to assess the model quality and defined the best predictor variables and the best spatial extent for each predictor variable (i.e. the extent for which adjusted R-square was highest). In a second step, we calculated multivariate models including all 5 predictor variables at each spatial extent. We also calculated a multiscale model including all 5 predictor variables at the spatial extent for which the adjusted R-square in the univariate model was highest (spatial extent of strongest effect). We compared model quality between all the multivariate models using adjusted R-square (as they use different data sets but with the same number of variables). We selected the most parsimonious multiscale model using the Akaike criterion (AIC).

Results

Vegetation changes

Effect of spatial extent on the absolute difference in vegetation changes (between a given extent and 25 m chosen as the reference) was significant for the five predictor variables, both in the open habitat data set and in the woodland data set (each ANOVA with $p < 0.001$).

Bird response

In 1978 mean bird species richness within a cluster was 10.59 ± 3.75 (mean \pm SD) for open habitat species and 10.59 ± 4.80 for woodland species. In 2003 it was 10.05 ± 3.64 and 8.62 ± 2.15 , respectively. The mean number of colonizing open habitat and woodland species was 2.32 ± 2.68 and 2.28 ± 2.44 , respectively per cluster. The mean proportion of species going extinct per cluster was 0.25 ± 0.18 for open habitat species and 0.28 ± 0.20 for woodland species.

Open habitat species showed strong variation in the performance of univariate models (Fig. 3A–B). For the proportion of species going extinct, the variable bare ground performed better at small scales (highest adjR^2 at 25 m = 42%, Fig. 3A), whereas for colonisation, the quality of model using tree cover increased when spatial extent increased (highest adjR^2 at 500 m = 23%, Fig. 3B). Open habitat species also showed important variation in the performance of multivariate models among spatial extents: the performance of the extinction model was highest at the local scale (highest adjR^2 at 25 m = 59%, Fig. 4A), whereas

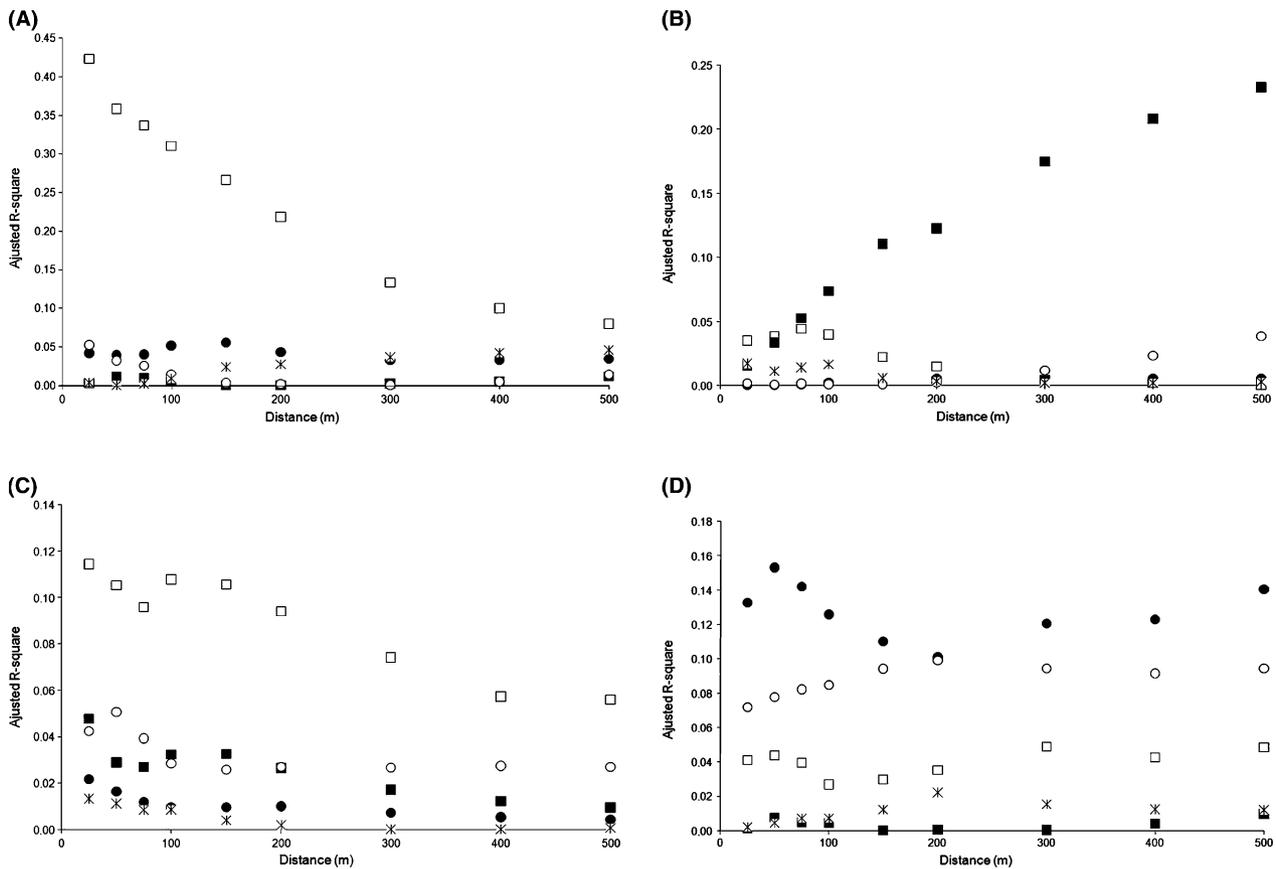


Figure 3. Model quality (adjusted R^2) of the different univariate models (□ bare ground, ○ herb, ● shrub, ■ tree and * heterogeneity): (A) extinction of open habitat species; (B) colonisation of open habitat species; (C) extinction of woodland species; (D) colonisation of woodland species.

the colonisation model performed better for the largest spatial extent (highest $\text{adj}R^2$ at 500 m = 37%, Fig. 4A). Both univariate and multivariate models of woodland species showed constancy in model quality for a variety of spatial extents and for all the predictor variables (Fig. 3C–D and Fig. 4B).

Multi-scale models showed a lower or equivalent quality than single-scale models for open habitat species, whereas multi-scale models performed better than single-scale models for woodland species, both for colonisation ($\text{adj}R^2 = 30\%$) and extinction ($\text{adj}R^2 = 18\%$), (Fig. 4A–B).

The most parsimonious models selected by AIC and parameters associated are shown in Table 2. For open habitat species, local extinction decreased with the decrease in local proportion of bare ground (slope = 0.014; Table 2; Fig. 5a) and local colonisation decreased with the increase in the proportion of trees at the landscape scale (slope = -0.088 ; Table 2). There was no significant model selected for the extinction of woodland species (Table 2). Colonisation of woodland species increased with the local increase in shrub cover (slope = 0.053; Table 2) and decreased when vegetation diversity increased at large scale (slope = -2.807 ; Table 2).

As a decrease of extinction rate in open habitat species with a decrease of bare ground was contrary to our predictions, we conducted further analyses of our dataset.

These complementary analyses showed that clusters with a low decrease in bare ground also presented a low cover of bare ground in 1981 (Fig. 5b) and a low number of open habitat species (Fig. 5c) while the clusters with a high decrease in bare ground presented a high cover of bare ground and a high number of open habitat species in 1981.

Discussion

Colonisation versus extinction, two distinct processes

This study showed that colonisation was multi-scale dependent. Colonisation of woodland species was likely to occur only when both local (high cover of shrub) and landscape conditions (low vegetation diversity, corresponding to a high connectivity in woodland habitat) were favourable. Such patterns of colonisation have to be investigated further with respect to “complementation” and “supplementation” processes which assume that some species either require access to different habitat types to complete their life cycle, or can compensate the low availability of an optimal habitat by using surrogate habitats (Dunning et al. 1992). Such processes are likely to be involved in the patterns of habitat use in many species living in heterogeneous human modified landscapes. For open

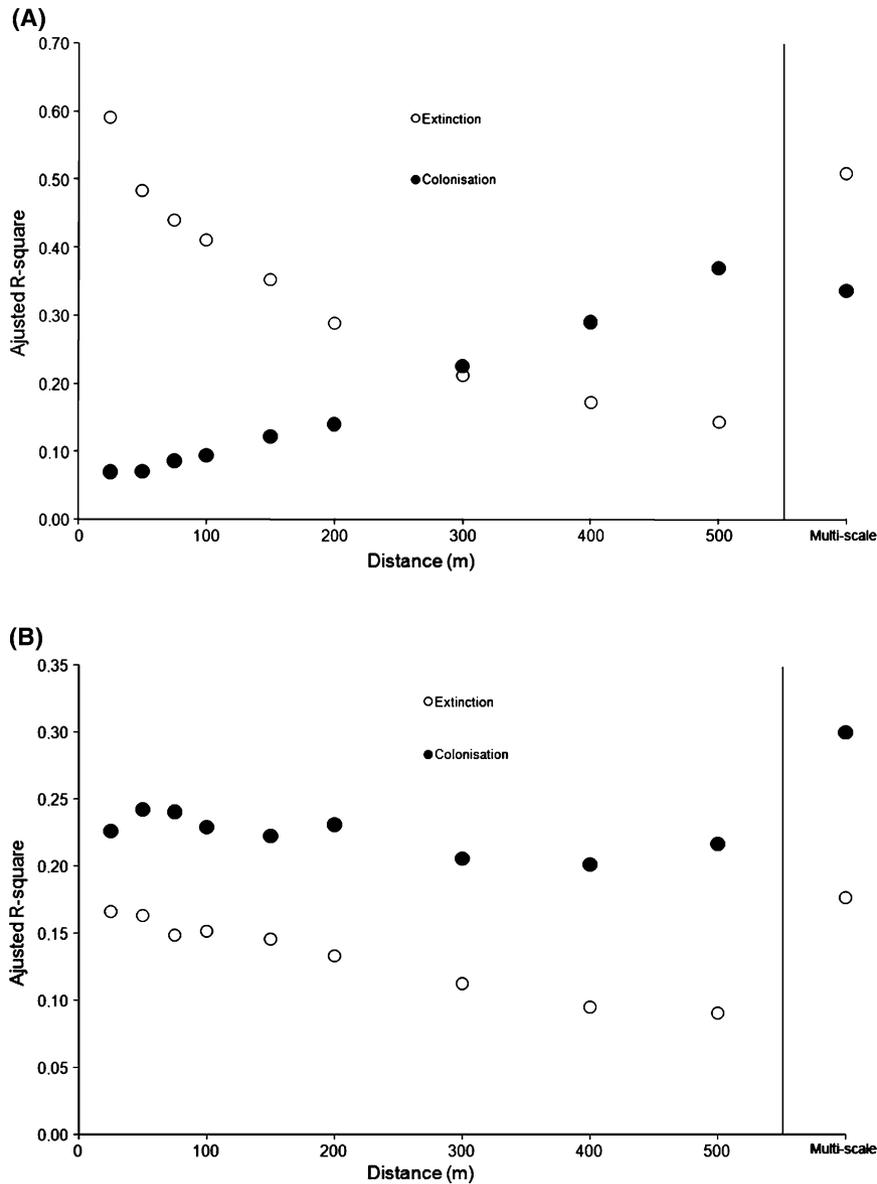


Figure 4. Model quality (adjusted R^2) of the different multivariate single-scale models and the multi-scale model: (A) open habitat species; (B) woodland species.

habitat species, colonisation occurred mainly when the vegetation remained open at the landscape scale (79 ha) rather than at the local scale, in particular when there was no or only little increase in tree cover. This could partly be related to the large average territory size of open habitat species or, more speculatively, to behavioural processes in habitat selection (e.g. public information, i.e. the use of the local reproductive performance of conspecifics as a cue in the selection of breeding habitat (Doligez et al. 2002)). Open habitat species are mainly Mediterranean species, which are also characterised by short-distance dispersal (Blondel and Aronson 1999, Brotons et al. 2005). Thus, dispersal processes could also explain some of the patterns observed and need to be further investigated (Brotons et al. 2005). As large open areas and their most typical bird species (e.g. *Alauda arvensis*) had already disappeared from our study area by 1978, we were not able to include true grassland specialists as a specific group within our open

habitat species. Because true grassland specialists are often sensitive to patch size and landscape composition (Hamer et al. 2006), we speculate that their colonisation pattern would have been associated even more strongly with larger scales. We also expect that they would have responded primarily to changes in cover of grass/shrub. On the other hand, our study showed that extinction of open habitat species did not depend on changes at multiple spatial extents. Extinction in these species mainly occurred when local conditions changed, whatever the landscape context. Contrarily to predictions, extinction of open habitat species was higher when the decrease in bare ground was minimal (Fig. 5a). But our dataset showed that clusters with a low decrease in bare ground were clusters already invaded by shrubs in 1981, while the clusters with a high decrease in bare ground were those with the most open vegetation in 1981. Extinction of open habitat species is thus maximal in the plots with a high cover of shrubs and a low cover of bare

Table 2. Parameters obtained for the most parsimonious models (lowest AIC) within multiscale models for extinction probability (extinction) and number of species colonizing (colonisation) (variable = variable of vegetation change selected in the model; spatial extent = spatial extent at which this variable is considered; slope = value of the slope of the linear regression; p = significance p-value of the regression; CI = confidence interval for the slope). Results for extinction of open habitat species are illustrated in Fig. 5a.

	Variable	Spatial extent	Slope	p	CI
Open habitat species					
extinction	bare ground	25	0.014	0.003	0.006–0.023
colonisation	tree	500	−0.088	0.036	−0.171–0.006
Woodland species					
extinction			no significant variable selected		
colonisation	shrub	50	0.053	0.005	0.017–0.089
	vegetation diversity	200	−2.807	0.038	−5.444–0.170

ground, i.e. in the later stages of the transitions from open habitat to shrubland. This result would have probably been different for grassland specialists. Their extinction would have been expected to be maximal in the early stage of land abandonment, when open areas start to be colonized by

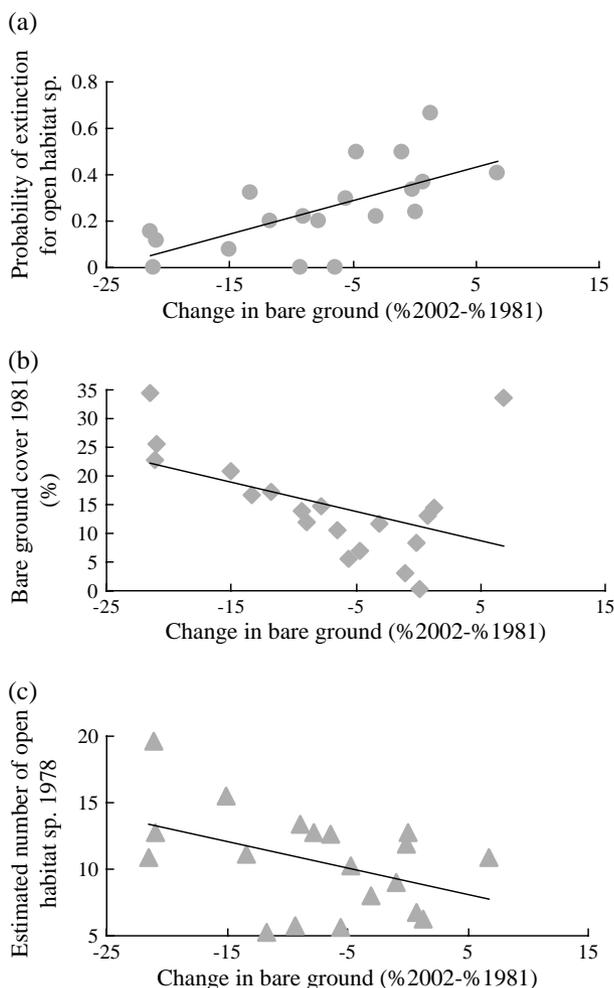


Figure 5. Relationships between change in bare ground cover between 1981 and 2002 and (a) extinction probability of open habitat species; (b) bare ground cover in 1981; (c) estimated number of open habitat species in 1978 (dots correspond to clusters; solid lines correspond to the regression: (a) $p=0.003$; slope = 0.014; (b) $p=0.046$; slope = -0.519 ; (c) $p=0.066$; slope = -0.196).

shrubs. Extinction of open habitat species was linked to vegetation changes at a very local spatial extent (0.2 ha), that was smaller than the minimum territory size (1 ha, Cramp and Perrins 1993). This suggests that species were able to persist in small remaining patches of suitable habitat in landscapes that became progressively fragmented. This could partly result from site fidelity (Matthiopoulos et al. 2005) an aspect that would deserve further study. The contrasting results on patterns of colonisation and extinction observed across a range of spatial extents emphasize how our understanding of species-habitat relationships will depend on the context a population lives in and on landscape dynamics. Habitat requirements derived from studies on declining populations are likely to correspond to habitats with low suitability and to reflect local scale processes, while requirements derived from expanding populations are likely to correspond to highly optimal habitats and to reflect multi-scale processes. As a consequence management objectives designed for declining populations might be inadequate.

Species from different habitats are sensitive to different vegetation features

Species from the two habitat types we studied, exhibited different patterns of response to vegetation change. Colonisation and extinction of bird species from open habitats were relatively well described by the information obtained from aerial photographs: our models explained over half of the total variance contained in the data. Model quality of woodland species showed no such marked dependence on the spatial extent considered. This pattern may be related to a lack of sensitivity of woodland species to specific spatial extents and result from the response to the combined effects of the vegetation changes that take place at different scales (Cushman and McGarigal 2004). This hypothesis is partly supported by our results, which indicate that colonisation of woodland species was best explained by the multiscale model. A second explanation could be that woodland species are sensitive to other vegetation variables than those extracted from aerial photographs. Indeed, vegetation classification of aerial photographs describes the horizontal vegetation cover but ignores the variation in vertical structure, which is critically important for bird from forested habitat (Prodon and Lebreton 1981). This explanation is supported by the relatively low amount of variance explained in the models of woodland species in

comparison to those of open habitat species, and by the lack of significant models for extinction of woodland species. Moreover, our unpublished data indicate that, contrary to open habitat species, the distribution of woodland bird species in 2003 was best explained by field recorded measures of the vertical structure of the vegetation within 25 m than by GIS data within 25 m (Sirami 2006). The contrast between the two species groups considered in the dependence of the model quality on the spatial extent considered emphasises the value of studying species groups separately when looking for patterns and the necessity to use multi-scale approaches when studying species-habitat relationships, a fortiori when considering different taxa (Allen and Starr 1982).

Effect of spatial extent on pattern detection

The strength of vegetation changes and the strength of the relationship between bird species colonisation/extinction (at least for open habitat species) and vegetation changes varied dramatically with respect to the spatial extent considered. Our results emphasize the need to account for the spatial extent when measuring vegetation changes and analysing species-habitat relationships. Until now, more attention had been given to the effects of a change in grain size (resolution of a map) than to those of a change in spatial extent (spatial area considered to measure patterns). Wu (2004) showed that effects of changing grain size were more predictable than those of changing spatial extent. However, the spatial extent considered in our study was limited by the study design and thus encompassed relatively local variations (from 25 to 500 m corresponding to 0.2 to 79 ha). Given the large home range of some of the species considered (e.g. *Alectoris rufa*), local colonisation and extinction processes are likely to be influenced by spatial extents > 500 m (Naveh and Lieberman 1984). For individual species which perceive environmental features at a very broad scale the effect of spatial extent on model quality with environmental variables is already well known (e.g. *Tetrao urogallus* for which the best model uses grain sizes of up to 250 ha (Graf et al. 2005)).

Conclusion

The spatial extent at which species respond to temporal changes in habitat is species dependent and will differ for colonisation and extinction dynamics. Many studies have analysed the effects of landscape on biodiversity (Atauri and de Lucio 2001, Dauber et al. 2003), but often a scale of sensitivity of the species is not included explicitly in the analysis (but see Suarez-Seoane and Baudry 2002, Chust et al. 2004). Our approach may help introduce spatial extent in an explicit, structured fashion in habitat management. This could be particularly useful to understand extinction thresholds, which are known to be influenced by landscape changes (Keymer et al. 2000). In the light of landscape change driven by land abandonment, our results show that considering spatial extent of vegetation changes is particularly important for declining species that depend on shrinking habitat, such as species that depend on open land

in the Mediterranean region (Preiss et al. 1997). Management for such species should aim at securing large areas of open habitat characterized by an abundance of local patches with a high cover of bare soil. Managing clear cutting and grazing at the landscape scale could allow creating such conditions (DeGraaf and Yamasaki 2003). Further studies on patterns shared among guilds should focus on process understanding (Bishop and Myers 2005) and on integrative multi-species conservation strategies at the scale of the landscape (Jepsen et al. 2005). These management strategies should also take into account that over a short temporal scale local processes like site-fidelity and dispersal are likely to be of high relevance. In these cases, we may expect delays in the response of the species under interest to our management decisions. On the other hand, in the longer-term, regional processes could overcome changes at the landscape scale and changes in the regional species pool could then interfere with management actions. Our findings on the scale of colonisation/extinction for open habitat/woodland species are likely to be generalised to other systems. This may be the case in those systems for which the bird community is composed from open habitat specialists rather than woodland specialists. For example, preliminary studies suggest that patch size seems to affect grassland species more than woodland species in South African savannas (Skwono and Bond 2003).

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