

Do bird spatial distribution patterns reflect population trends in changing landscapes?

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Abstract Strong relations between population trends and spatial distribution have been suggested at the regional scale: declining species should have more fragmented distributions because decline causes range retractions towards optimal habitats, whereas increasing species should have more aggregated distributions, because colonization processes are constrained by distance. Most analyses of the effects of land use changes on animal populations are diachronic studies

of population dynamics or synchronic studies of species habitat selection. Few studies take simultaneously into account temporal changes in habitat distribution and changes in species spatial distribution. We applied the above rationale to the landscape scale and analysed how population declines, increases or stability, as diagnosed in a long term study, correlate with population connectivity or fragmentation at that scale. We used data on changes in faunal distribution and information on temporal changes in the vegetation in a Mediterranean area that had been subjected to land abandonment. We found that species declining at the landscape scale had retracting fragmented distributions and that expanding species had expanding continuous distributions. However, for the latter, we suggest that the factors involved are related to landscape structure and not to dispersal mediated meta-population processes, which are of little relevance at this local scale. We also show that even species that are numerically stable can show fragmentation of their distribution and major spatial distribution shifts in response to land use changes, especially in species that have low occurrence levels or that are associated with transitory habitats such as heterogeneous shrublands (e.g. *Sylvia melanocephala*). Studying the spatial structure of species distribution patterns at the landscape scale may provide information about population declines and increases both at the regional and the landscape scale and can improve our understanding of short-term risks of local extinction.

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Introduction

In the current context of rapid modifications in land use patterns, a major challenge for ecology and conservation is to understand how these will affect biodiversity. Land use changes have been shown to affect species distributions of many groups and to lead to noticeable turnover of species at landscape (mosaic of vegetation patches corresponding to several km²) and regional (i.e. mosaic of ecosystems corresponding to 10⁴ km²) scales [e.g. plants (Lavergne et al. 2005); birds (Chamberlain and Fuller 2000)]. Land use changes are also likely to have contrasting effects on different species (Preiss et al. 1997; Burel et al. 2004; Moreira et al. 2005; Sirami et al. 2007). The diagnosis of the consequences of land use changes on animal population trends can either result directly from an assessment of population trends through diachronic studies of population dynamics (Sirami et al. 2007) or, indirectly, from synchronic studies of species habitat selection coupled with the prediction of expected population consequences that would result from changes in habitat availability (Suarez-Seoane et al. 2002). The latter approach, however, does not take into account the additional demographic effects that changes in landscape structure are likely to have on the dynamics of spatial population processes such as colonisation and extinction rates in local patches (Hanski 1999) and more generally on the demographic health of the remnant populations. So far, very few studies have tried to link patterns of temporal changes in spatial distribution with temporal trends in species occurrence (increase or decline) at the landscape scale.

Strong relations between population trends and spatial distribution have been suggested at the regional scale (Wilson et al. 2004): declining species should have more fragmented distributions (i.e. change from a continuous distribution to a discontinuous distribution, with an increase in the number of patches of continuous presence, and a decrease in their size; Fig. 1) because decline causes range retractions towards optimal habitats at local scales (Thomas et al. 2008), whereas species that increase should have

more continuous distributions (i.e. change from a discontinuous distribution to a more continuous one, with a decrease in the number of patches of continuous presence, but an increase in their size), because colonization processes are constrained by distance.

We applied this rationale to the landscape scale to analyse how population declines, increases or stability, as diagnosed in a long term study, correlated with temporal changes in species spatial distribution (increased connectivity or fragmentation) at that scale. We assumed that, at this scale, factors involved would be related to changes in the landscape structure and vegetation distribution rather than to dispersal mediated meta-population processes which are of little relevance at such a local scale.

We predicted that species with similar temporal occurrence trends (1) should show similar changes in spatial distribution and (2) that these changes should be consistent with patterns of change in vegetation distribution. As a corollary, patterns of temporal change in spatial distribution could serve as a proxy to assess population trends in the absence of quantitative population data.

We combined long-term data on faunal distribution in a study area in Mediterranean France with information on temporal changes in vegetation extracted from aerial photographs to address four questions: (1) What are the temporal changes in the spatial patterns of land cover categories? (2) Do species with similar occurrence trends show similar spatial dynamics? (3) What is the role of species attributes in these spatial dynamics? (4) Do species spatial dynamics track vegetation dynamics?

The study area we selected has been subjected to land abandonment since the middle of the twentieth century. Decreases in grazing intensity and woodland exploitation have led to a widespread increase in woody vegetation at the landscape scale: woodlands have expanded while grasslands have retracted and became more fragmented (Sirami et al. 2007).

We used information on songbird distribution that had been recorded at three points in time over a period of 25 years (1978, 1992 and 2003) to identify three groups of species in relation to temporal trends in their occurrence rate: increasing, declining and stable (Sirami et al. 2007). We expected the distribution of increasing species to show one or several of the following dynamics: expansion of the existing distribution patches, colonisation of new areas and

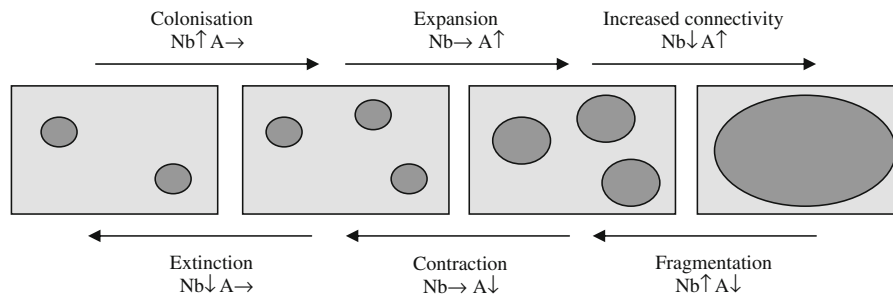


Fig. 1 Illustration of the changes in spatial distribution of population (Nb number of areas with continuous distribution; A average size of these polygons; \uparrow = increase and \downarrow = decrease)

increase in the degree of spatial connectivity. Conversely, we expected the distribution of declining species to show one or several of the following dynamics: fragmentation of the existing distribution and contraction of the remaining patches of continuous presence (illustrated in Fig. 1). We expected stable species to be either generalist species showing little sensitivity to vegetation changes or specialist species whose habitat amount is remaining constant (Litvaitis 1993). We predicted generalist stable species to have unchanged spatial distributions and little sensitivity to the changes in the vegetation. We predicted specialist species associated with specific habitat features to show shifts in their spatial distribution but remain stable in their proportion in the landscape. Finally, instability of a species' spatial distribution could be expected in the case of more generalist species with densities well below saturation. The spatial distribution of their territories could shift from 1 year to the next as a consequence of a random process of individual establishment (Maron et al. 2005).

Methods

Study area and vegetation dynamics

The study area was situated 20 km north of Montpellier (southern France) (43°47'N, 03°50'E). It covers 2,800 ha and is a typical Mediterranean mosaic of grasslands and croplands embedded within a matrix of shrublands and woodlands (for further details see Preiss et al. (1997); Sirami et al. (2007)). Grasslands were maintained by extensive sheep grazing until the middle of the twentieth century. Shrublands were also

used for grazing sheep and for the production of juniper oil. The oak woodlands were coppiced at 30-year intervals for charcoal until the last peak of intensive use during World War II (Debussche et al. 1987).

Around the 1960s, technological advances, trade globalization, and the creation of the European community all negatively affected the profitability of sheep farming in the region, resulting in a period of rapid land abandonment 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).

Bird community sampling and change

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. 2). At each plot, birds were censused once in each of the three study years. In 1978 we used a randomized order of visit of the plots, 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 censused by means of 20 min point counts with unlimited distance (Bibby et al. 1992). 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.

Gonzalo-Turpin et al. (2008) showed, using the PRESENCE software (MacKenzie et al. 2002), that

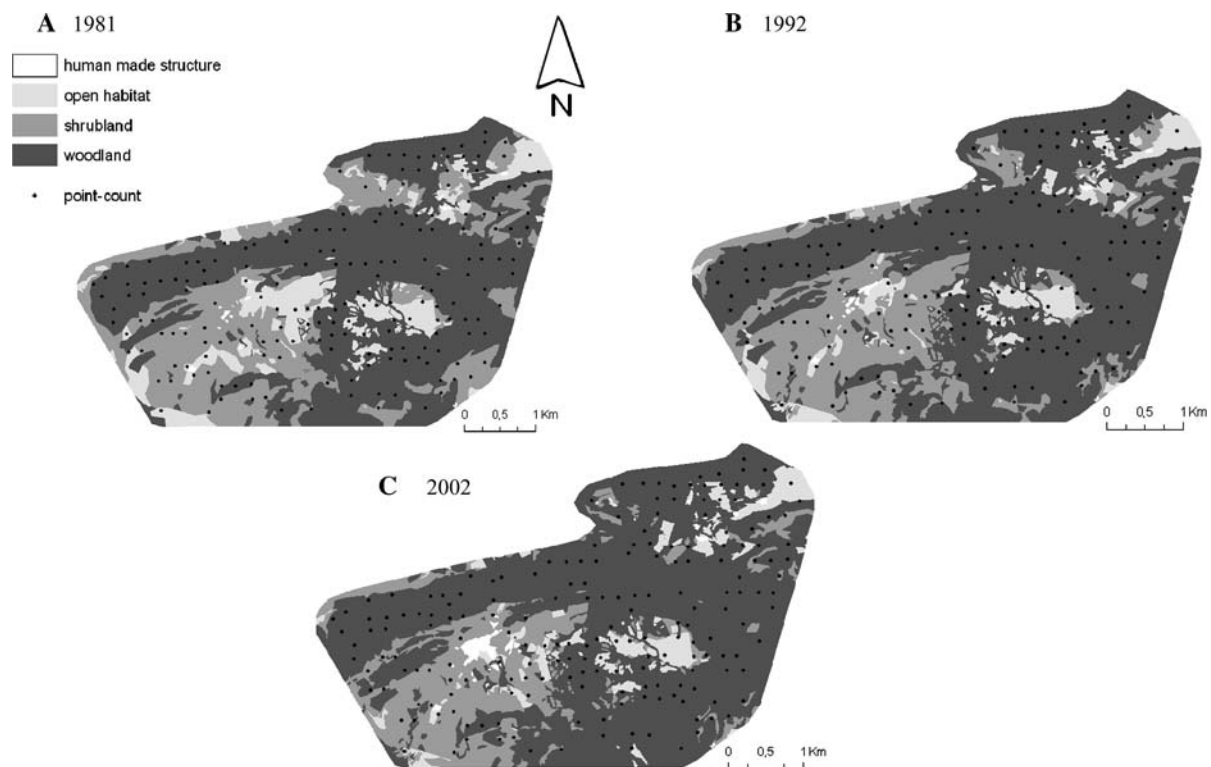


Fig. 2 Location of the 194 census-plots and land cover map for 1981, 1992 and 2002 (simplified from Sirami et al. 2007)

detectability biases caused by observer (confounded with year), wind velocity, cloud cover, date and sampling hour as well as vegetation structure did not significantly affect occupancy rate estimations based on 20-min long point counts. We therefore considered that such biases should have negligible effects on occurrence rates in our study.

Species were considered increasing, declining or stable according to their change in occurrence (defined as the rate of presence–absence at the landscape level) between 1978 and 2003 that was estimated in Sirami et al. (2007). Temporal change in species occurrence was assessed using generalized estimating equations (GEE, SAS version 8; SAS Institute Inc. 1999). Species that changed significantly in occurrence rate between 1978 and 2003 were considered decreasing or increasing (Table 1). Species that did not show a significant change in occurrence rate between 1978 and 2003 but showed significant opposite trends during the two intermediate periods (1978–1992, 1992–2002) were considered non-consistent. Species that did not show a significant change in occurrence rate over the entire period

of study (between 1978 and 2003) and that did not show significant opposite trends during the two intermediate periods (1978–1992, 1992–2002) were considered stable. We did not analyse species that had inconsistent trends (*Sylvia cantillans* and *Cuculus canorus*).

In keeping with the changes in the vegetation, 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. Of nine species relying on closed woodlands, the occurrence rate of seven increased significantly, while it decreased for two (Sirami et al. 2007).

Bird species distribution maps

We drew species distribution maps by spatial interpolation of raw data using kriging of the species occurrence data for each of the three dates studied using the Geostatistical Analyst extension to ARCGIS 9 (Environmental Systems Research Institute,

Table 1 Bird species ordered by their numerical trends (Sirami et al. 2007)

		Total area (ha)			Polygon nb			Polygon size (ha)			Occ	Hab	H.b.
		1978	1992	2003	1978	1992	2003	1978	1992	2003			
Decreasing	<i>Emberiza hortulana</i>	213	106	–	3	2	–	71	53	–	20	–1.86	0.71
	<i>Lanius senator</i>	180	81	4	3	3	2	60	27	2	17	–1.90	0.27
	<i>Serinus serinus</i>	405	98	136	5	2	1	81	49	136	49	–0.73	0.47
	<i>Sylvia undata</i>	1,308	168	96	4	2	3	327	84	32	76	–0.79	0.63
	<i>Carduelis chloris</i>	528	27	60	4	3	2	132	9	30	50	–0.86	0.44
	<i>Turdus merula</i>				1	1	1				178		0.56
Increasing	<i>Lulula arborea</i>				1	1	3				51		0.67
	<i>Hypolais polyglotta</i>				1	3	2				44		0.50
	<i>Certhia brachydactyla</i>	39	66	720	1	3	5	39	22	144	41	0.82	0.50
	<i>Columba palumbus</i>	–	244	396	–	4	11	–	61	36	42	0.59	0.54
	<i>Parus caeruleus</i>	192	272	462	3	4	6	64	68	77	32	0.64	0.51
	<i>Parus major</i>	1,008	1,414	1,470	7	2	3	144	707	490	108	0.26	0.58
	<i>Regulus ignicapillus</i>	56	1,040	1,536	8	4	2	7	260	768	99	0.87	0.52
	<i>Sylvia atricapilla</i>	1,155	1,485	2,088	3	1	1	385	1,485	2,088	130	0.66	0.50
	<i>Fringilla coelebs</i>	2,033	2,557	2,612	1	1	1	2,033	2,557	2,612	194	0.19	0.52
	Stable	<i>Phylloscopus collybita</i>	70	39	160	2	1	5	35	39	32	13	0.94
<i>Carduelis carduelis</i>		208	55	385	8	1	11	26	55	35	28	–0.86	0.44
<i>Aegithalos caudatus</i>		240	335	232	8	5	4	30	67	58	36	0.35	0.50
<i>Garrulus glandarius</i>		189	240	192	7	4	4	27	60	48	43	0.53	0.52
<i>Upupa epops</i>		32	32	54	4	2	3	8	16	18	10	–0.22	0.47
<i>Emberiza cirius</i>		330	668	318	5	4	6	66	167	53	45	–1.25	0.53
<i>Sylvia melanocephala</i>		1,236	1,648	1,278	3	2	3	412	824	426	96	–0.15	0.46
<i>Erithacus rubecula</i>		741	750	1,360	3	6	2	247	125	680	98	0.85	0.56
<i>Luscinia megarhynchos</i>		2,518	2,333	2,268	1	1	1	2,518	2,333	2,268	171	0.04	0.54
<i>Sylvia hortensis</i>		909	906	749	3	3	7	303	302	107	67	–0.68	0.68
<i>Streptopelia turtur</i>		1,484	1,252	1,340	2	4	4	742	313	335	86	0.13	0.51
<i>Oriolus oriolus</i>		234	203	92	1	1	4	234	203	23	18	–1.44	0.50
<i>Emberiza calandra</i>		349	239	144	1	1	3	349	239	48	23	–1.76	0.51
<i>Pica pica</i>		117	195	108	1	3	4	117	65	27	27	–0.89	0.40
<i>Alectoris rufa</i>		812	856	640	4	4	5	203	214	128	64	–0.45	0.42
<i>Phylloscopus bonelli</i>	176	120	56	4	3	2	44	40	28	27	0.10	0.51	

Total area (ha) = total size of polygons in hectare in 1978, 1992 and 2003; Polygon nb = number of polygons in 1978, 1992 and 2003; Polygon size = average polygon size in hectare in 1978, 1992 and 2003; Occ = maximum number of census-plots in which the species was recorded; Hab = species score on the first axis of the co-inertia analysis published by Sirami et al. (2007) (a low score characterizes a species selecting open habitats; a high score a species selecting closed forested habitats); H.b. = habitat breadth used in Sirami et al. (2008) (a low score corresponds to specialist species; a high score corresponds to generalist species)

Inc.). Kriging, a geostatistical procedure based on the regionalized variable theory assuming constant spatial variation throughout the prediction area, predicts the z -value (P/A) of unsampled locations from a weighted combination of sampled points throughout the study area (Legendre and Fortin 1989). Kriging

therefore assumes that the spatial variation in the species distribution is statistically homogeneous with respect to all variables throughout the surface except for distance between the points. Indicator kriging can be used to interpolate presence–absence data (Burrough and McDonnell 1998), but it requires an

a priori threshold to transform the surface of presence probabilities into a presence–absence map. Instead, we used a method allowing us to select the most relevant threshold for each species and each year. We checked for spatial trends in species distributions using the tool provided in the Geostatistical Analyst extension to ARCGIS 9 (Environmental Systems Research Institute, Inc.). Only ten species were associated with a spatial trend, only in 1 year or with contradictory trends between years. As there was no reason for a particular spatial trend and the difference between universal and ordinal kriging has been shown to be non significant in many cases (e.g. Carr and Roberts 1989), we used ordinary kriging for all species and all years. The spatial variation was quantified by the semi-variogram computed from the input point dataset (194 points; presence or absence was associated with the pixel in the centre of the census-plot). The semi-variance was calculated based upon the average variance of all point pairs within distance intervals that were adjusted automatically to have a sufficient number of point pairs in the first distance interval (Johnston et al. 2001). We fitted a spherical model of the semi-variogram to the empirical semi-variogram (Fig. 3). We used the five nearest neighbors to predict the presence, estimated between zero and one, for unmeasured locations using the default cell size defined by ARCGIS 9. We transformed the surface obtained into a distribution map (polygons associated with presence or absence) using the ROC (receiver operating characteristic) curve, minimizing abs (sensitivity–specificity) in R (R Development Core Team 2008) in order to choose the best threshold value to define presence and absence for each species and each year (Hanley and McNeil 1982).

The use of a single visit to predict species distributions can lead to false presences and false absences and thus produce inaccurate distribution maps. However, detectability biases did not significantly affect occupancy rate estimations in our dataset (see Gonzalo-Turpin et al. 2008). Moreover, to confirm that the use of a single visit during a single year did not affect the distribution maps, we used a complementary dataset on bird species distribution in 2004 and 2005 for 50 of the 194 census points sampled in 1978 and 2003 (unpublished). Eighty percent of the observations were consistent during the three consecutive years (2003, 2004 or 2005). We

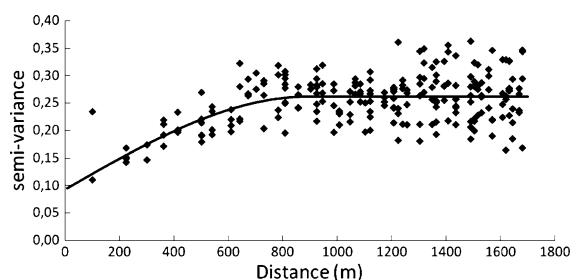


Fig. 3 Example of the semi-variogram used in the kriging method (*Sylvia melanocephala* in 1992): the *dots* correspond to the empirical semi-variogram, the *line* corresponds to the spherical model fitted to the empirical semi-variogram

therefore considered that the spatial interpolation of our species occurrence data allowed accurate distribution maps.

For each species, we obtained three maps describing its spatial distribution in 1978, 1992 and 2003. Then we realized a fourth map for each species, corresponding to the intersection of the three maps. For this fourth map, we considered polygons of less than 1,000 pixels (i.e., 0.05 ha) as artefacts of the geostatistical procedures and excluded them from the analyses. We assessed temporal changes in species distribution using polygon change analysis defined by Sadahiro and Umemura (2000). We considered the following types of polygons: (1) *generation*: the species is present but was absent at the previous date, (2) *disappearance*: the species is absent but was present at the previous date, (3) *persistence*: the species is present and was present at the previous date, (4) *absence*: the species is absent and was absent at the previous date.

Land cover map

To describe the general context of temporal changes in landscape composition and structure, we used the land cover maps obtained from the interpretation of the 1981, 1992 and 2002 aerial photographs used by Sirami et al. (2007). The landscape dynamics in this region are mainly driven by vegetation succession and thus relatively slow. In addition wild fires are rare in this part of the Mediterranean. In the absence of documented fires and other major perturbation, we considered that the vegetation on these photographs was a reasonable proxy for the state of the vegetation in the years the birds were surveyed. Our land cover

maps identified polygons corresponding to seven land cover types after visual interpretation. We separated polygons representing human-made structures and grouped the six remaining land cover types into three land cover categories including each two of the initial land cover types: open habitat (grassland and crops), shrubland (open and closed), woodland (open and closed) (Fig. 2).

Vegetation map

To relate bird spatial dynamics to fine-scale vegetation spatial dynamics, we described changes in the vegetation composition in the four types of polygons defined above. We used the vegetation maps obtained from a pixel classification of the 1981, 1992 and 2002 aerial photographs used by (Sirami et al. 2007). In these maps, each pixel (0.7×0.7 m) is associated to one of the four classes: bare soil (little or no vegetation), herb (herbaceous vegetation), shrub (woody vegetation 0.5–2.5 m) and tree (woody vegetation >3 m). We calculated the cover percentage of tree, shrub, herb and bare soil for each year and each polygon in each species distribution map.

Analyses

Landscape changes

We calculated the total area, number of polygons and average polygon size for the three main land cover categories (open habitat, shrubland and woodland) and for each year.

To assess the temporal changes in the location of land cover categories we calculated the amount of overlap between polygons of the same land cover category between different years (1981–1992, 1992–2002, 1981–2002). The *relative area overlap* was defined by Maruca and Jacquez (2002) as $RAO_{ij} = a_{(i \cap j)} / a_{(i \cup j)}$, where $a_{(i \cap j)}$ is the area of intersection and $a_{(i \cup j)}$ is the area of union for polygons at the beginning of the time interval (i) and at the end of the time interval (j). RAO for non-intersecting polygons is zero, and increasing values represent better overlap, with a maximum value of 1. Because we were interested in, and expected, temporal changes in the location of land cover categories we also calculated the *relative area generation* defined as $RAG_{ij} = (a_i - a_{(i \cap j)}) / a_{(i \cup j)}$ where a_j is the area of

polygon at the end of the time interval, and the *relative area disappearance* defined as $RAD_{ij} = (a_i - a_{(i \cap j)}) / a_{(i \cup j)}$ where a_i is the area of polygon at the beginning of the time interval, i . We calculated these three indices for each land cover category and each time interval (1981–1992, 1992–2002 and 1981–2002).

Bird species distribution changes

We calculated the total area occupied by each species for each year. As species trends were based on changes in the number of occurrence, we obviously expected total area occupied and occurrence to be proportional. We also calculated the number of polygons and average polygon size occupied by each species for each year (using the distribution map for each year 1978, 1992 and 2003). Then, we assessed temporal changes in bird species spatial distribution (using the fourth map corresponding to the intersection of the three previous maps). We calculated the three indices defined for land cover categories *relative area overlap* (RAO), *relative area generation* (RAG) and the *relative area disappearance* (RAD) for each species and each time interval (1978–1992, 1992–2003 and 1978–2003). In order to test whether species with different long-term trends showed different temporal changes in the location of the polygons occupied, we compared these three variables (RAO , RAG and RAD) between the three groups of species (decreasing, increasing and stable) using a Kruskal–Wallis ANOVA.

Role of biological attributes

In order to understand potential temporal changes in the location of the polygons occupied by species considered stable, we assessed the role of population dynamics and biological attributes on the *relative area overlap area* of these species. We used linear regressions to test whether the species *relative area overlap* (RAO) was affected (1) by the occurrence of these species at the landscape scale (as defined by the maximum number of census-plots where the species were recorded during 1 year); (2) by the habitat they select (as defined by the species' score on the first axis of the co-inertia analysis in Sirami et al. (2007))—a low score characterizes a species that selects open habitats; a high score a species that

selects closed forested habitats—and (3) by their habitat breadth, as defined in Sirami et al. (2008).

Role of vegetation changes

In order to assess the relationships between temporal changes in the location of polygons occupied by the bird species and vegetation characteristics, we tested whether the different types of polygons (absence; generation; persistence; disappearance) presented different vegetation covers. We calculated for all polygons the percent cover of the 4 pixel classes (tree, shrub, herb and bare soil) for each year. All the vegetation values were weighted by the percentage of the study area represented by the corresponding polygon.

We calculated vegetation characteristics in the different types of polygons for each species and analysed the differences for each species group: increasing, decreasing and stable. In order to simplify the analyses and results, we tested for differences in vegetation characteristics only for the following polygon types: (1) for increasing species, absence and generation polygons; (2) for declining species, persistence and disappearance polygons; (3) for species considered stable, appearance and disappearance polygons. For each species group (increasing, declining and stable), we compared vegetation characteristics between the two types of polygons defined, at the beginning and the end of the interval considered, using a *U*-Mann–Whitney test.

Results

Landscape changes

The number of Woodland polygons increased and the median of their size increased (Table 2). The number of Open habitat and Shrubland polygons increased while the median of their size decreased. Woodlands were characterised by a high percentage of overlap of polygons between years (average RAO 99%) whereas Open habitat and Shrubland showed a much lower overlap of polygons between years (average RAO respectively 71 and 66%; Table 1). Woodlands were associated with a high percentage of generation of new polygons (RAG), Open habitats with a high percentage of existing polygons that disappeared (RAD) while Shrublands showed a high percentage of both disappearance of existing polygons and generation of new polygons (Table 2).

Bird distribution changes

Of the increasing species, three (*Certhia brachydactyla*, *Columba palumbus* and *Parus caeruleus*) showed an increase in the number of polygons with little variation or an increase in the mean polygon size (Table 1), as in the colonisation scenario illustrated in Fig. 1. Three species (*Parus major*, *Regulus ignicapillus* and *Sylvia atricapilla*; Fig. 4a) showed a decrease in the number of polygons used and an increase of the mean polygon size (Table 1), as in the

Table 2 Characteristics of the spatial distribution of the three main land cover categories in 1981, 1992 and 2002 (number of polygons and polygon size—median and range in hectares) and their dynamics over 1981–1992, 1992–2002 and 1981–2002

	Polygon nb			Polygon size (ha)			Polygon dynamics			
	1981	1992	2002	1981	1992	2002	RAD	RAO	RAG	
Open habitat	11	11	12	0.50 (0.03–2,046)	0.69 (0.04–1,479)	0.21 (0.04–1,653)	81–92	38	62	6
							92–02	3	97	17
							81–02	46	54	9
Shrubland	11	15	16	1.32 (0.02–4,971)	0.57 (0.07–5,024)	0.25 (0.07–3,867)	81–92	26	74	17
							92–02	30	70	8
							81–02	46	54	18
Woodland	11	13	12	0.38 (0.02–8,349)	1.17 (0.04–11,430)	1.69 (0.04–12,072)	81–92	1	99	14
							92–02	1	99	11
							81–02	1	99	24

RAD Relative area disappearance, *RAO* relative area overlap, *RAG* relative area generation corresponding to the percentage of the distribution, respectively disappearing, persisting or being generated (Cf. methods)

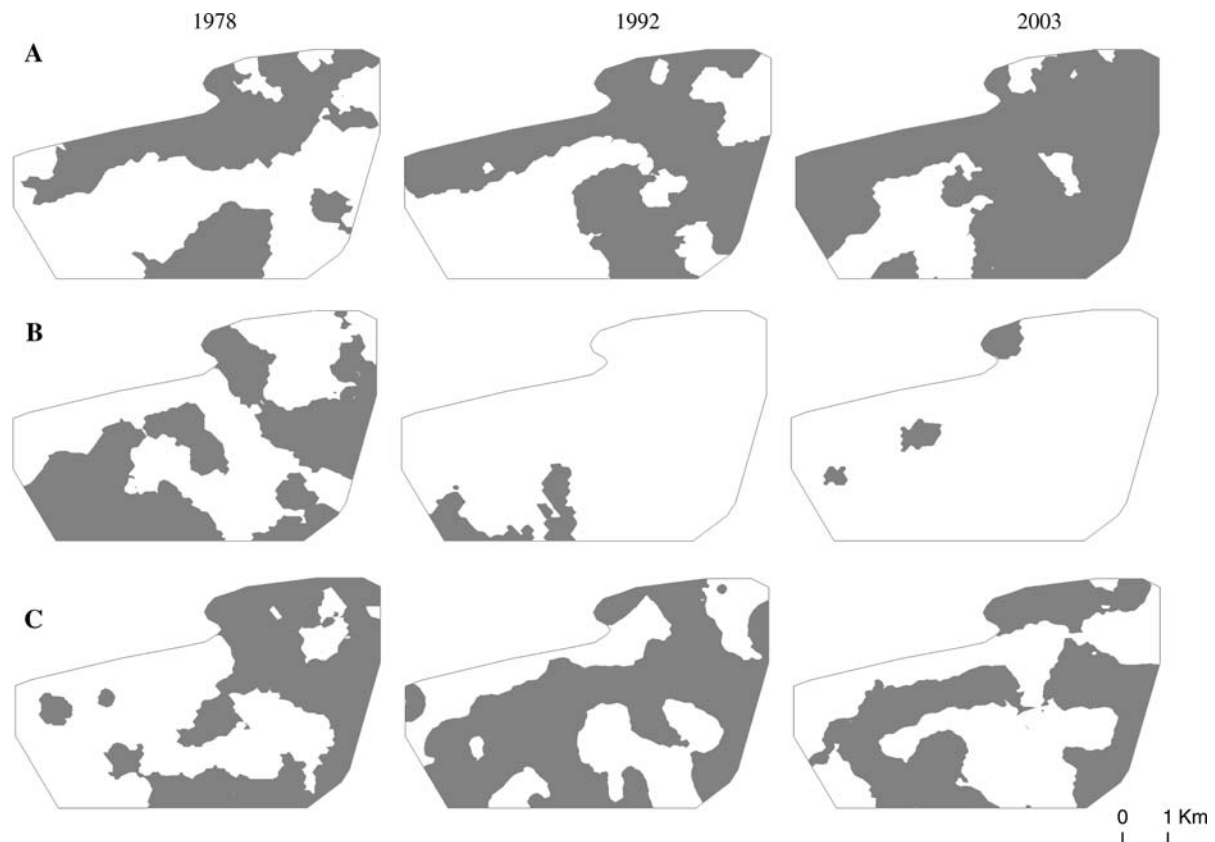


Fig. 4 Examples of distribution map in 1978, 1992 and 2003 for **a** increasing species (*Sylvia atricapilla*); **b** decreasing species (*Sylvia undata*); **c** stable species (*Sylvia melanocephala*). The shaded areas correspond to the modelled species presence

scenario of increasing connectivity illustrated in Fig. 1. The range of one species, *Fringilla coelebs*, consisted of a single polygon that increased in size (Table 1).

All decreasing species showed a decrease both in the number of polygons predicted and in their mean size (Fig. 4b, as in the contraction/extinction scenario in Fig. 1, except *Serinus serinus* (Table 2). The apparent increase in mean patch size for *Serinus serinus* was actually due to the disappearance of four small polygons between 1978 and 1992.

Within stable species, two species (*Phylloscopus collybita* and *Carduelis chloris*) showed an increase in the number of polygons forming their range (colonisation scenario illustrated in Fig 1); three species (*Upupa epops*, *Aegithalos caudatus* and *Garrulus glandarius*) showed a decrease in the number of polygons and an increase in the mean polygon size (scenario of increasing connectivity illustrated in Fig 1); four species showed no or little change in

the number of polygons and in mean polygon size (Fig. 4c); six species (*Oriolus oriolus*, *Emberiza calandra*, *Pica pica*, *Sylvia hortensis*, *Streptopelia turtur* and *Alectoris rufa*) showed an increase in the number of polygons forming their range and a decrease in their mean size (fragmentation scenario illustrated in Fig 1) and one species (*Phylloscopus bonelli*) showed a decrease both in the number of polygons used and in their mean size (contraction scenario illustrated in Fig. 1) (Table 1).

The three groups of species showed significant differences in the percentage of polygons that overlapped (Kruskal–Wallis ANOVA; $P = 0.022$), in the existing polygons that disappeared (Kruskal–Wallis ANOVA; $P = 0.022$) and in the number of new polygons generated (Kruskal–Wallis ANOVA; $P = 0.000$). Increasing species showed a higher percentage of polygons that overlapped between the beginning and the end of the intervals considered (Kruskal–Wallis ANOVA; $P = 0.019$), a lower

percentage of polygons that disappeared (Kruskal–Wallis ANOVA; $P = 0.019$), and a higher percentage of polygons generated between years (Kruskal–Wallis ANOVA; $P = 0.019$) than decreasing species (Table 3). Stable species showed intermediate values, not significantly different from the values for the increasing species (Kruskal–Wallis ANOVA; $pRAD = 0.268$; $pRAO = 0.268$; except for the percentage of new polygons generated $pRAG = 0.000$) or from the values of decreasing species (Kruskal–Wallis ANOVA; $pRAD = 0.351$; $pRAO = 0.351$; $pRAG = 0.079$; Table 3).

Role of biological attributes

Among stable species, the percentage of polygons that overlapped between years (RAO) increased with bird species occurrence rate (linear regression; $P < 0.001$, slope = 0.46). Species habitat had no significant effect on the percentage of polygon overlap between years (linear regression; $P = 0.51$). Finally, the percentage of polygon overlap between years increased with species habitat breadth (linear regression; $P = 0.01$, slope = 161.70).

Role of vegetation changes

For increasing species, polygons in which a species appeared (generation) had higher tree cover and lower shrub and herb cover than polygons where the species was absent (absence) at the beginning or at the end of the time interval. Polygons where the species appeared also had a lower bare soil cover at the end date (Fig. 5a).

For decreasing species, polygons where the species remained present (persistence) had a lower tree cover than polygons where the species disappeared (disappearance), both at the beginning and at the end of the time interval (Fig. 5b). Polygons where the species remained present also had a higher herb cover at the beginning of the time interval and a higher shrub cover at the end of the time interval (Fig. 5b).

For stable species, polygons where the species appeared (generation) and polygons where the species disappeared (disappearance) did not show any significant difference, either at the beginning or at the end of the time interval (Fig. 5c). As the heterogeneity of this group of species was likely to explain the absence of a significant difference, we conducted

further analyses using three sub-groups of stable species: stable-expansionist (5 stable species associated with scenarios of colonisation or increasing connectivity illustrated in Fig. 1), stable-contractionist (7 stable species associated with contraction + extinction scenarios illustrated in Fig. 1) and stable-stable (4 stable species associated with no change in distribution characteristics). For stable-expansionists species, polygons where the species appeared (generation) had a significantly lower tree cover at the beginning of the time interval and higher shrub cover at the end of the time interval than observed in absence polygons (Fig. 5d). Stable-contractionists species showed results similar to decreasing species: polygons where the species remained present (persistence) had a significantly lower tree cover and a significantly higher herb cover than polygons where the species disappeared (disappearance), both at the beginning and at the end of the time interval (Fig. 5e). For stable-stable species, polygons where the species appeared (generation) had a significantly higher shrub cover at the beginning of the time interval than polygons where the species disappeared (disappearance; Fig. 5f).

Discussion

Distribution dynamics related to species characteristics

Our results support the view that, at the landscape scale, the spatial dynamics of species distribution are related to the temporal dynamics of species occurrence.

Increase in species occurrence was associated with either colonisation, expansion or increasing connectivity of their spatial distribution. The spatial dynamics of increasing species were consistent with their habitat associations as well. For instance, *Fringilla coelebs*, considered a generalist species (Cramp and Perrins 1993), was already widespread in the study area at the onset of the study and continued to expand its distribution. *Parus major*, *Regulus ignicapillus* and *Sylvia atricapilla*, associated with woodlands (Cramp and Perrins 1993), were present in the initial woodland patches and their respective distributions became more continuous as woodland patches merged due to woodland expansion. Finally, species such as *Certhia brachydactyla*, *Columba palumbus*

Table 3 Spatio-temporal dynamic of species distribution for each group (decreasing, increasing and stable species; according to their change in occurrence between 1978 and 2003

(Sirami et al. 2007) over 1981–1992, 1992–2002 and 1981–2002 (corresponding to the three lines per species)

Decreasing species	RAD	RAO	RAG	Increasing species	RAD	RAO	RAG	Stable species	RAD	RAO	RAG
<i>Carduelis chloris</i>	98	2	3	<i>Certhia brachydactyla</i>	100	0	185	<i>Aegithalos caudatus</i>	95	5	133
	100	0	233		11	89	976		97	3	66
	97	3	8		1	99	1872		96	4	92
<i>Emberiza hortulana</i>	70	30	18	<i>Columba palumbus</i>	-	-	-	<i>Alectoris rufa</i>	48	52	53
	-	-	-		71	29	135		57	43	32
	-	-	-		-	-	-		61	39	40
<i>Lanius senator</i>	89	11	34	<i>Fringilla coelebs</i>	2	98	28	<i>Carduelis carduelis</i>	91	9	16
	100	0	5		1	99	3		67	33	698
	99	1	1		1	99	30		63	37	148
<i>Serinus serinus</i>	97	3	21	<i>Hippolais polyglotta</i>	30	70	3801	<i>Emberiza calandra</i>	45	55	13
	35	65	74		55	45	18		77	23	38
	100	0	33		100	0	2433		71	29	12
<i>Sylvia undata</i>	89	11	1	<i>Lulula arborea</i>	68	32	36	<i>Emberiza cirrus</i>	24	76	126
	100	0	58		69	31	300		62	38	9
	94	6	1		36	64	162		56	44	52
<i>Turdus merula</i>	12	88	2	<i>Parus caeruleus</i>	53	47	95	<i>Erithacus rubecula</i>	39	61	41
	6	94	14		61	39	130		20	80	101
	6	94	2		71	29	212		29	71	112
				<i>Parus major</i>	27	73	67	<i>Garrulus glandarius</i>	80	20	105
					38	62	42		97	3	78
					38	62	83		87	13	88
				<i>Phylloscopus collybita</i>	100	0	52	<i>Luscinia megarhynchos</i>	11	89	3
					100	0	443		10	90	7
					38	62	0		13	87	3
				<i>Sylvia atricapilla</i>	26	74	54	<i>Oriolus oriolus</i>	31	69	17
					6	94	47		61	39	6
					7	93	88		67	33	6
								<i>Phylloscopus bonelli</i>	95	5	63
									100	0	48
									98	2	30
								<i>Pica pica</i>	52	48	119
									83	17	41
									90	10	85
								<i>Regulus ignicapillus</i>	46	54	14
									98	2	4
									97	3	1
								<i>Sylvia hortensis</i>	25	75	25
									35	65	17
									41	59	23
								<i>Sylvia melanocephala</i>	19	81	48
									50	50	25
									45	55	42
								<i>Streptopelia turtur</i>	45	55	29
									37	63	44
									45	55	36
								<i>Upupa epops</i>	100	0	95
									100	0	176
									95	5	0
Average	74	26	32		44	56	452		61	39	64
Standard error	37	37	58		34	34	917		29	29	103

RAD Relative area disappearance, RAO relative area overlap, RAG relative area generation (in percent)

and *Parus caeruleus*, which require bigger or more mature trees for nesting and/or feeding (Cramp and Perrins 1993), colonized new favourable patches that progressively appeared as woodlands matured. Our

study suggests that, at the landscape scale, the temporal dynamics of the spatial distribution of increasing species are mainly controlled by the patterns of expansion of their preferred habitats.

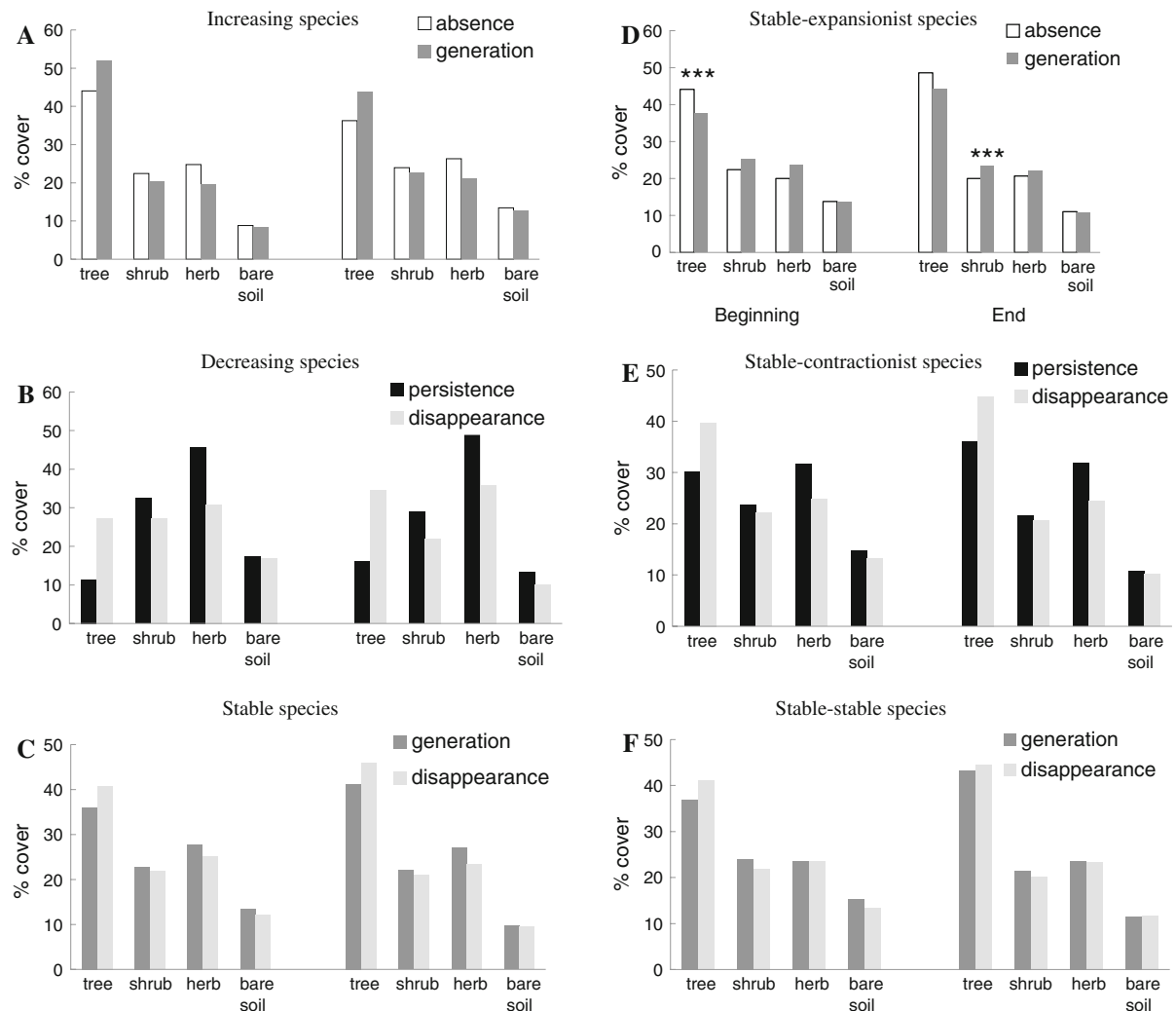


Fig. 5 Comparison of vegetation cover (tree, shrub, her, bare soil) at the beginning and end of the time interval considered (1978–1992, 1992–2003 or 1978–2003) for contrasting types of polygons: **a** Increasing species; **b** Decreasing species; **c**

Stable species; **d** Stable expansionist species; **e** Stable contractionist species; **f** Stable-stable species. *** indicate significant difference ($P = 0.05$)

Contrary to the regional scale where metapopulation processes control the patterns of expansion (Wilson et al. 2004; Brotons et al. 2005) dispersal constraints are unlikely to occur at the landscape scale (Paradis et al. 1998).

Decrease in species occurrence was associated with distribution contractions (illustrated in Fig. 1). All declining species were already in the last stage of habitat loss: the contraction of existing occupied polygons (Hanski 1999) resulting from the loss of open habitats (Sirami et al. 2007). This study suggests

that the distribution patterns of declining species result from the retractions in range following contraction of optimal habitats (Johnson 1998). This result had also been found at the regional (Wilson et al. 2004) scale, suggesting that declining species follow the same processes at both scales.

Stability in species occurrence was associated with diverse spatial dynamics of their distributions. Only four of the 16 stable species kept a constant distribution pattern through time. In this study, seven species showed fragmentation or contraction of their

distribution although the change was not significant. This result is consistent with their ecological requirements (species associated with shrubland and open habitat, negative or low scores on axis 1 of the co-inertia; Table 2) and suggests that these species are likely to undergo a future decrease in occurrence if the landscape becomes more forested.

Landscape factors behind distribution dynamics

Most species appeared to respond significantly to changes in land cover patterns at the landscape scale. Over the decades considered, the spatial distribution of most species showed little persistence and this was correlated to vegetation change. The persistence or non-persistence of a given part of the species range (polygon) was significantly explained by this polygon's vegetation composition. Although some of the differences in vegetation cover were small, they were all consistent with the past land cover dynamics and species habitat requirements. In the context of abandonment and landscape closure, wooded habitats were either stable or expanding (Sirami et al. 2007). Thus, woodland-associated bird species tended to increase in occurrence and to expand their distribution. In addition, once they were present in a location, they tended to continue to be observed there. The low percentage of persistence of open habitats was largely due to the spatial and temporal dynamics of traditional grazing activities in the Mediterranean region (Farina 1995). Under the current regime of land abandonment species tied to open habitats showed simultaneously an overall trend of range contraction and of little temporal overlap of their distribution between years. Finally, stable species included a range of species associated with the whole gradient of habitats (Sirami et al. 2007), and thus a diversity of patterns of spatial distribution changes. However, the patterns of the three subclasses were consistent with the prediction that spatial distribution is tracking vegetation changes (Fig. 5d–f). Stable species showed slightly higher percentage of persistence of their distribution over years than decreasing species. Stable species with a low occurrence rate at the landscape scale showed a lower percentage of persistence of their distribution over years, which is consistent with a random distribution within potentially favourable polygons (Maron et al. 2005). The lower percentage of persistence of the distribution of

specialist species may be explained by a higher proportion of specialist species associated with transitory habitats such as heterogeneous shrubland (e.g. *Sylvia melanocephala*, Fig. 4c).

Lessons for conservation

All the decreasing species in our study were already showing marked population fragmentation at the onset of our long term study and were experiencing the last stage of habitat loss. This suggests that fragmentation of distribution at the landscape scale occurs early in the process of species decline and that taking spatial dynamics of species distribution into account in a context of land use changes could allow better and earlier assessment of species vulnerability. As vegetation was not taken into account in the methods we used to obtain species distribution, our study is likely to underestimate fragmentation due to the presence of unsuitable habitat within the predicted species distribution. As a result, this emphasizes the endangered status of the five declining species studied in this paper (*Emberiza hortulana*; *Lanius senator*; *Serinus serinus*; *Sylvia undata*; *Carduelis chloris*) as fragmentation of the remaining open habitats will facilitate the establishment and growth of woody species (Debussche and Lepart 1992) and further increase the risk of local extinction within these remaining patches. Our results also suggest that studying the spatial structure of species distribution patterns may provide information about population dynamics not only at the regional (Wilson et al. 2004) but also at the landscape scale. Spatial analyses also showed that, contrary to the trends of their occurrence rates, species considered stable were highly and potentially negatively affected by land use changes. As a result they could be experiencing the early stages of population decline and should be included in management policies. Thus proper knowledge of temporal changes in distribution may help predict species vulnerability even in the absence of solid data on numerical trends.

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