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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.

Keywords (separated by '-') Long-term trend - Spatial dynamic - Fragmentation - Connectivity - Bird

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

4 Clélia Sirami · Lluís Brotons · Jean-Louis Martin

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9 regional scale: declining species should have more
10 fragmented distributions because decline causes range
11 retractions towards optimal habitats, whereas increas-
12 ing species should have more aggregated distributions,
13 because colonization processes are constrained by
14 distance. Most analyses of the effects of land use
15 changes on animal populations are diachronic studies

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species habitat selection. Few studies take simulta- 17
neously into account temporal changes in habitat 18
distribution and changes in species spatial distribution. 19
We applied the above rationale to the landscape scale 20
and analysed how population declines, increases or 21
stability, as diagnosed in a long term study, correlate 22
with population connectivity or fragmentation at that 23
scale. We used data on changes in faunal distribution 24
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in a Mediterranean area that had been subjected to land 26
abandonment. We found that species declining at the 27
landscape scale had retracting fragmented distribu- 28
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distribution shifts in response to land use changes, 37
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heterogeneous shrublands (e.g. *Sylvia melanocephala*). 40
Studying the spatial structure of species distribution 41
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improve our understanding of short-term risks of local 45
extinction. 46

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47 **Keywords** Long-term trend · Spatial dynamic ·
48 Fragmentation · Connectivity · Bird

49
50 **Introduction**
51

52 In the current context of rapid modifications in land
53 use patterns, a major challenge for ecology and
54 conservation is to understand how these will affect
55 biodiversity. Land use changes have been shown to
56 affect species distributions of many groups and to
57 lead to noticeable turnover of species at landscape
58 (mosaic of vegetation patches corresponding to
59 several km²) and regional (i.e. mosaic of ecosystems
60 corresponding to 10⁴ km²) scales [e.g. plants (Laver-
61 gne et al. 2005); birds (Chamberlain and Fuller
62 2000)]. Land use changes are also likely to have
63 contrasting effects on different species (Preiss et al.
64 1997; Burel et al. 2004; Moreira et al. 2005; Sirami
65 et al. 2007). The diagnosis of the consequences of
66 land use changes on animal population trends can
67 either result directly from an assessment of popula-
68 tion trends through diachronic studies of population
69 dynamics (Sirami et al. 2007) or, indirectly, from
70 synchronic studies of species habitat selection cou-
71 pled with the prediction of expected population
72 consequences that would result from changes in
73 habitat availability (Suarez-Seoane et al. 2002). The
74 latter approach, however, does not take into account
75 the additional demographic effects that changes in
76 landscape structure are likely to have on the dynam-
77 ics of spatial population processes such as colonisa-
78 tion and extinction rates in local patches (Hanski
79 1999) and more generally on the demographic health
80 of the remnant populations. So far, very few studies
81 have tried to link patterns of temporal changes in
82 spatial distribution with temporal trends in species
83 occurrence (increase or decline) at the landscape
84 scale.

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

continuous distributions (i.e. change from a discon-
95 tinuous distribution to a more continuous one, with a
96 decrease in the number of patches of continuous
97 presence, but an increase in their size), because
98 colonization processes are constrained by distance.
99

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

110 We predicted that species with similar temporal
111 occurrence trends (1) should show similar changes in
112 spatial distribution and (2) that these changes should
113 be consistent with patterns of change in vegetation
114 distribution. As a corollary, patterns of temporal
115 change in spatial distribution could serve as a proxy
116 to assess population trends in the absence of quan-
117 titative population data.

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

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

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

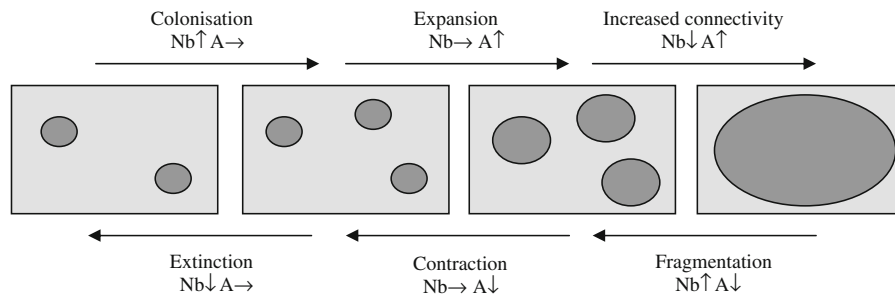


Fig. 1 Illustration of the changes in spatial distribution of population (Nb number of areas with continuous distribution; A average size of these polygons; \uparrow = increase and \downarrow = decrease)

144 increase in the degree of spatial connectivity. Con-
 145 versely, we expected the distribution of declining
 146 species to show one or several of the following
 147 dynamics: fragmentation of the existing distribution
 148 and contraction of the remaining patches of contin-
 149 uous presence (illustrated in Fig. 1). We expected
 150 stable species to be either generalist species showing
 151 little sensitivity to vegetation changes or specialist
 152 species whose habitat amount is remaining constant
 153 (Litvaitis 1993). We predicted generalist stable species
 154 to have unchanged spatial distributions and little
 155 sensitivity to the changes in the vegetation. We
 156 predicted specialist species associated with specific
 157 habitat features to show shifts in their spatial
 158 distribution but remain stable in their proportion in
 159 the landscape. Finally, instability of a species' spatial
 160 distribution could be expected in the case of more
 161 generalist species with densities well below saturation.
 162 The spatial distribution of their territories could shift
 163 from 1 year to the next as a consequence of a random
 164 process of individual establishment (Maron et al. 2005).

165 Methods

166 Study area and vegetation dynamics

167 The study area was situated 20 km north of Montpel-
 168 lier (southern France) (43°47'N, 03°50'E). It covers
 169 2,800 ha and is a typical Mediterranean mosaic of
 170 grasslands and croplands embedded within a matrix of
 171 shrublands and woodlands (for further details see
 172 Preiss et al. (1997); Sirami et al. (2007)). Grasslands
 173 were maintained by extensive sheep grazing until the
 174 middle of the twentieth century. Shrubbylands were also
 175 used for grazing sheep and for the production of

juniper oil. The oak woodlands were coppiced at
 176 30-year intervals for charcoal until the last peak of
 177 intensive use during World War II (Debussche et al.
 178 1987).
 179

180 Around the 1960s, technological advances, trade
 181 globalization, and the creation of the European
 182 community all negatively affected the profitability
 183 of sheep farming in the region, resulting in a period of
 184 rapid land abandonment with a strong decrease in
 185 sheep grazing and the abandonment of oak coppicing.
 186 As a result, significant vegetation changes occurred in
 187 the study area during the study period (1978–2003):
 188 open habitats (grasslands and shrublands) declined
 189 dramatically while woodlands increased (Sirami et al.
 190 2007).

191 Bird community sampling and change

192 The bird community was surveyed at 194 census-
 193 plots defined in 1978 by Preiss et al. (1997) with a
 194 minimum distance of 250 m between plots (Fig. 2).
 195 At each plot, birds were censused once in each of the
 196 three study years. In 1978 we used a randomized
 197 order of visit of the plots, and followed the same
 198 order in 1992 and 2003 so as to be consistent in the
 199 timing of the bird community sampling among the
 200 three periods. Birds were censused by means of
 201 20 min point counts with unlimited distance (Bibby
 202 et al. 1992). We excluded from the analysis all
 203 species that were recorded only in 5 plots or less, as
 204 their presence was likely to be the result of stochastic
 205 factors or of the presence of highly specific habitat
 206 features not relevant to the present study. As a result,
 207 we were left with 34 species.

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

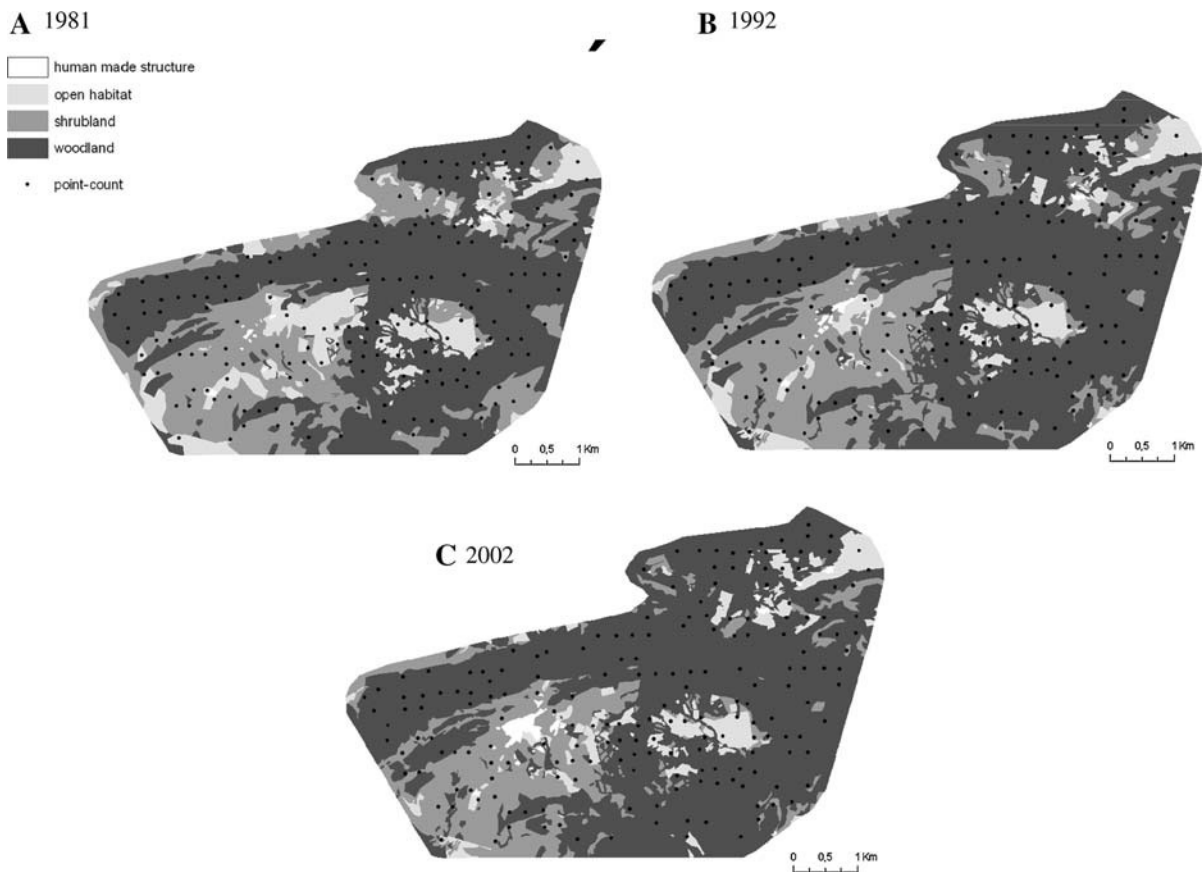


Fig. 2 Location of the 194 census-plots and land cover map for 1981, 1992 and 2002 (simplified from Sirami et al. 2007)

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

217 Species were considered increasing, declining or
218 stable according to their change in occurrence
219 (defined as the rate of presence-absence at the
220 landscape level) between 1978 and 2003 that was
221 estimated in Sirami et al. (2007). Temporal change in
222 species occurrence was assessed using generalized
223 estimating equations (GEE, SAS version 8; SAS
224 Institute Inc. 1999). Species that changed signifi-
225 cantly in occurrence rate between 1978 and 2003
226 were considered decreasing or increasing (Table 1).
227 Species that did not show a significant change in
228 occurrence rate between 1978 and 2003 but showed

229 significant opposite trends during the two intermedi-
230 ate periods (1978–1992, 1992–2002) were considered
231 non-consistent. Species that did not show a signifi-
232 cant change in occurrence rate over the entire period
233 of study (between 1978 and 2003) and that did not
234 show significant opposite trends during the two
235 intermediate periods (1978–1992, 1992–2002) were
236 considered stable. We did not analyse species that
237 had inconsistent trends (*Sylvia cantillans* and *Cuculus*
238 *canorus*).

239 In keeping with the changes in the vegetation,
240 there was an overall shift of the bird community in
241 favour of woodland species (Sirami et al. 2007). Of
242 seven species dependent on open habitats, the occur-
243 rence rate of five decreased significantly whereas it
244 increased for two species. Of nine species relying on
245 closed woodlands, the occurrence rate of seven
246 increased significantly, while it decreased for two
247 (Sirami et al. 2007).

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 brachyactyla</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 cirrus</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)

248 Bird species distribution maps

249 We drew species distribution maps by spatial inter-
 250 polation of raw data using kriging of the species
 251 occurrence data for each of the three dates studied
 252 using the Geostatistical Analyst extension to ARC-
 253 GIS 9 (Environmental Systems Research Institute,

Inc.). Kriging, a geostatistical procedure based on the 254
 regionalized variable theory assuming constant spa- 255
 tial variation throughout the prediction area, predicts 256
 the z -value (P/A) of unsampled locations from a 257
 weighted combination of sampled points throughout 258
 the study area (Legendre and Fortin 1989). Kriging 259
 therefore assumes that the spatial variation in the 260

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

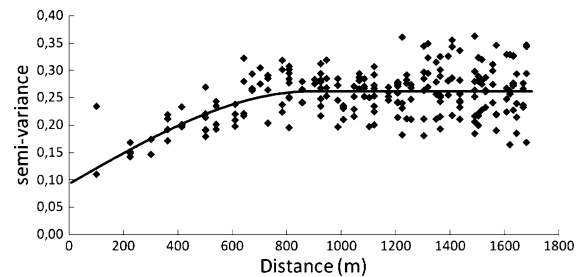


Fig. 3 Example of the semi-variogram used in the kriging method (*Sylvia melanocephala* in 1992): the dots correspond to the empirical semi-variogram, the line corresponds to the spherical model fitted to the empirical semi-variogram

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 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 Umermura (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

343 in this part of the Mediterranean. In the absence of
 344 documented fires and other major perturbation, we
 345 considered that the vegetation on these photographs
 346 was a reasonable proxy for the state of the vegetation
 347 in the years the birds were surveyed. Our land cover
 348 maps identified polygons corresponding to seven land
 349 cover types after visual interpretation. We separated
 350 polygons representing human-made structures and
 351 grouped the six remaining land cover types into three
 352 land cover categories including each two of the initial
 353 land cover types: open habitat (grassland and crops),
 354 shrubland (open and closed), woodland (open and
 355 closed) (Fig. 2).

356 Vegetation map

357 To relate bird spatial dynamics to fine-scale vegetation
 358 spatial dynamics, we described changes in the vege-
 359 tation composition in the four types of polygons
 360 defined above. We used the vegetation maps obtained
 361 from a pixel classification of the 1981, 1992 and 2002
 362 aerial photographs used by (Sirami et al. 2007). In these
 363 maps, each pixel (0.7×0.7 m) is associated to one of
 364 the four classes: bare soil (little or no vegetation), herb
 365 (herbaceous vegetation), shrub (woody vegetation
 366 $0.5\text{--}2.5$ m) and tree (woody vegetation >3 m). We
 367 calculated the cover percentage of tree, shrub, herb and
 368 bare soil for each year and each polygon in each species
 369 distribution map.

370 Analyses

371 *Landscape changes*

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

376 To assess the temporal changes in the location of
 377 land cover categories we calculated the amount of
 378 overlap between polygons of the same land cover cat-
 379 egory between different years (1981–1992, 1992–
 380 2002, 1981–2002). The *relative area overlap* was
 381 defined by Maruca and Jacquez (2002) as $RAO_{ij} =$
 382 $a_{(i \cap j)} / a_{(i \cup j)}$, where $a_{(i \cap j)}$ is the area of intersection and
 383 $a_{(i \cup j)}$ is the area of union for polygons at the
 384 beginning of the time interval (i) and at the end of
 385 the time interval (j). RAO for non-intersecting
 386 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 $RAG_{ij} = (a_j - a_{(i \cap j)}) / a_{(i \cup j)}$ 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 intersec-
 tion of the three previous maps). We calculated the
 three indices defined for land cover categories
relative area overlap (RAO), *relative area genera-
 tion* (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
 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

432 were recorded during 1 year); (2) by the habitat
433 they select (as defined by the species' score on the
434 first axis of the co-inertia analysis in Sirami et al.
435 (2007))—a low score characterizes a species that
436 selects open habitats; a high score a species that
437 selects closed forested habitats—and (3) by their
438 habitat breadth, as defined in Sirami et al. (2008).

439 *Role of vegetation changes*

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

451 We calculated vegetation characteristics in the
452 different types of polygons for each species and
453 analysed the differences for each species group:
454 increasing, decreasing and stable. In order to sim-
455 plify the analyses and results, we tested for differences
456 in vegetation characteristics only for the following
457 polygon types: (1) for increasing species, absence
458 and generation polygons; (2) for declining species,
459 persistence and disappearance polygons; (3) for spe-
460 cies considered stable, appearance and disappearance

polygons. For each species group (increasing, declin- 461
ing and stable), we compared vegetation characteris- 462
tics between the two types of polygons defined at the 463
beginning and the end of the interval considered, using 464
a *U*-Mann–Whitney test. 465

466 **Results**

467 *Landscape changes*

468 The number of Woodland polygons increased and the 469
median of their size increased (Table 2). The number 470
of Open habitat and Shrubland polygons increased 471
while the median of their size decreased. Woodlands 472
were characterised by a high percentage of overlap of 473
polygons between years (average RAO 99%) whereas 474
Open habitat and Shrubland showed a much lower 475
overlap of polygons between years (average RAO 476
respectively 71 and 66%; Table 1). Woodlands were 477
associated with a high percentage of generation of 478
new polygons (RAG), Open habitats with a high 479
percentage of existing polygons that disappeared 480
(RAD) while Shrublands showed a high percentage 481
of both disappearance of existing polygons and 482
generation of new polygons (Table 2).

483 *Bird distribution changes*

484 Of the increasing species, three (*Certhia brachydac-* 485
tyla, *Columba palumbus* and *Parus caeruleus*) showed 486

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)

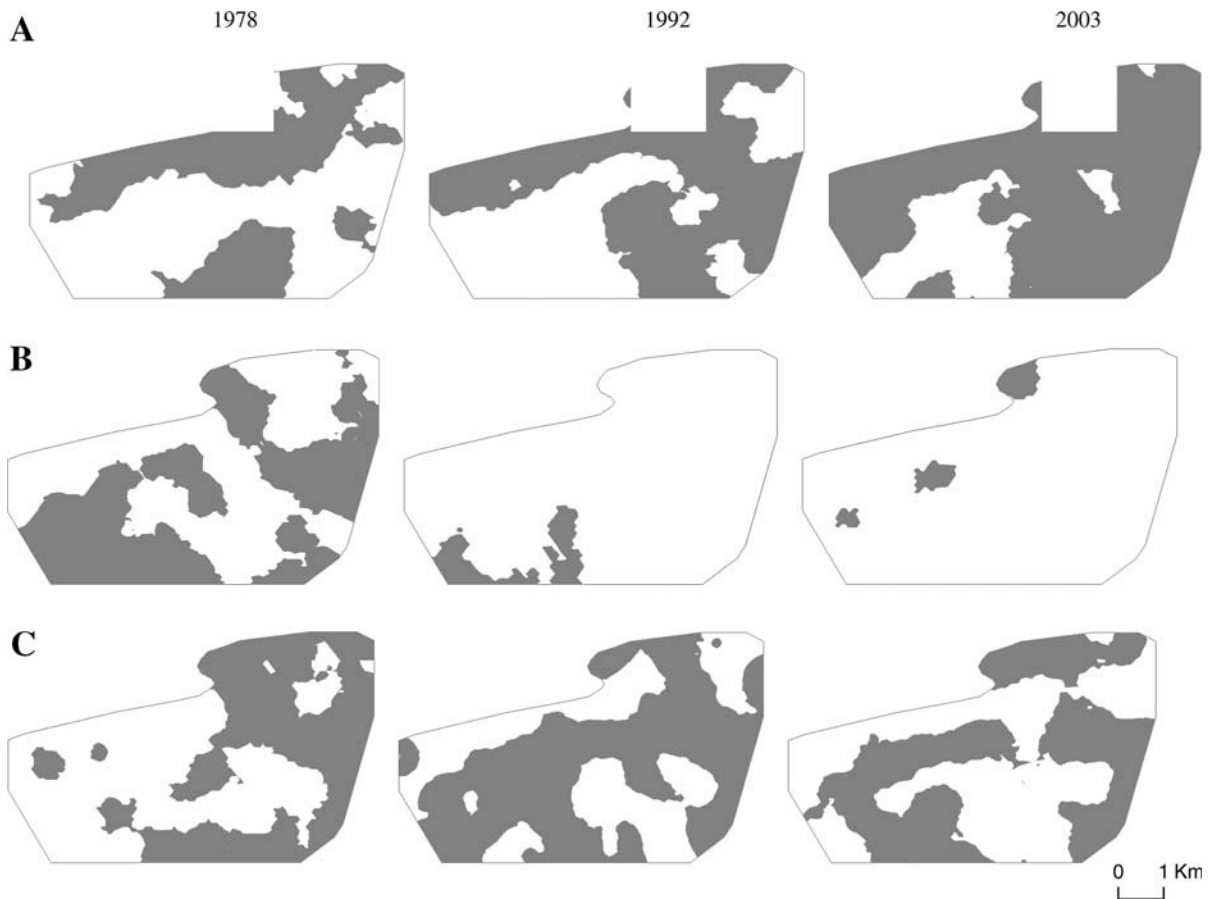


Fig. 4 Examples of distribution map in 1978, 1992 and 2003 for **a** increasing species (*Sylvia atricapilla*); **b** decreasing species (*Sylvia undata*); **c** stable species (*Sylvia melanocephala*). The shaded areas correspond to the modelled species presence

486 an increase in the number of polygons with little
 487 variation or an increase in the mean polygon size
 488 (Table 1), as in the colonisation scenario illustrated in
 489 Fig. 1. Three species (*Parus major*, *Regulus ignicap-*
 490 *illus* and *Sylvia atricapilla*; Fig. 4a) showed a decrease
 491 in the number of polygons used and an increase of the
 492 mean polygon size (Table 1), as in the scenario of
 493 increasing connectivity illustrated in Fig. 1. The range
 494 of one species, *Fringilla coelebs*, consisted of a single
 495 polygon that increased in size (Table 1).

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

503 Within stable species, two species (*Phylloscopus*
 504 *collybita* and *Carduelis chloris*) showed an increase
 505 in the number of polygons forming their range
 506 (colonisation scenario illustrated in Fig 1); three
 507 species (*Upupa epops*, *Aegithalos caudatus* and
 508 *Garrulus glandarius*) showed a decrease in the
 509 number of polygons and an increase in the mean
 510 polygon size (scenario of increasing connectivity
 511 illustrated in Fig 1); four species showed no or little
 512 change in the number of polygons and in mean
 513 polygon size (Fig. 4c); six species (*Oriolus oriolus*,
 514 *Emberiza calandra*, *Pica pica*, *Sylvia hortensis*,
 515 *Streptopelia turtur* and *Alectoris rufa*) showed an
 516 increase in the number of polygons forming their
 517 range and a decrease in their mean size (fragmenta-
 518 tion scenario illustrated in Fig 1) and one species
 519 (*Phylloscopus bonelli*) showed a decrease both in the

520 number of polygons used and in their mean size
521 (contraction scenario illustrated in Fig. 1) (Table 1).

522 The three groups of species showed significant
523 differences in the percentage of polygons that overlapped
524 (Kruskal–Wallis ANOVA; $P = 0.022$), in the
525 existing polygons that disappeared (Kruskal–Wallis
526 ANOVA; $P = 0.022$) and in the number of new
527 polygons generated (Kruskal–Wallis ANOVA; $P =$
528 0.000). Increasing species showed a higher percentage
529 of polygons that overlapped between the beginning and
530 the end of the intervals considered (Kruskal–Wallis
531 ANOVA; $P = 0.019$), a lower percentage of polygons
532 that disappeared (Kruskal–Wallis ANOVA; $P =$
533 0.019), and a higher percentage of polygons generated
534 between years (Kruskal–Wallis ANOVA; $P = 0.019$)
535 than decreasing species (Table 3). Stable species
536 showed intermediate values, not significantly different
537 from the values for the increasing species (Kruskal–
538 Wallis ANOVA; $pRAD = 0.268$; $pRAO = 0.268$;
539 except for the percentage of new polygons generated
540 $pRAG = 0.000$) or from the values of decreasing
541 species (Kruskal–Wallis ANOVA; $pRAD = 0.351$;
542 $pRAO = 0.351$; $pRAG = 0.079$; Table 3).

543 Role of biological attributes

544 Among stable species, the percentage of polygons
545 that overlapped between years (RAO) increased with
546 bird species occurrence rate (linear regression; $P <$
547 0.001 , slope = 0.46). Species habitat had no signif-
548 icant effect on the percentage of polygon overlap
549 between years (linear regression; $P = 0.51$). Finally,
550 the percentage of polygon overlap between years
551 increased with species habitat breadth (linear regres-
552 sion; $P = 0.01$, slope = 161.70).

553 Role of vegetation changes

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

561 For decreasing species, polygons where the spe-
562 cies remained present (persistence) had a lower tree
563 cover than polygons where the species disappeared
564 (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 spe-
cies disappeared (disappearance) did not show any
significant difference, either at the beginning or at the
end of the time interval (Fig. 5c). As the heteroge-
neity 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 associ-
ated with scenarios of colonisation or increasing
connectivity illustrated in Fig. 1), stable-contraction-
ist (7 stable species associated with contrac-
tion + extinction scenarios illustrated in Fig. 1) and
stable-stable (4 stable species associated with no
change in distribution characteristics). For stable-
expansionist species, polygons where the species
appeared (generation) had a significantly lower tree
cover at the beginning of the time interval and higher
shrubs cover at the end of the time interval than
observed in absence polygons (Fig. 5d). Stable-
contractionist 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 (disap-
pearance), 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 begin-
ning of the time interval than polygons where the
species disappeared (disappearance; Fig. 5f).

601 Discussion

602 Distribution dynamics related to species
603 characteristics

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

607 Increase in species occurrence was associated with
608 either colonisation, expansion or increasing connectiv-
609 ity of their spatial distribution. The spatial dynamics of

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	1,872		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
<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	3,801	<i>Emberiza calandra</i>	45	55	13
	35	65	74		55	45	18		77	23	38
	100	0	33		100	0	2,433		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	

Table 3 continued

Decreasing species	RAD	RAO	RAG	Increasing species	RAD	RAO	RAG	Stable species	RAD	RAO	RAG
								<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)

610 increasing species were consistent with their habitat
 611 associations as well. For instance, *Fringilla coelebs*,
 612 considered a generalist species (Cramp and Perrins
 613 1993), was already widespread in the study area at the
 614 onset of the study and continued to expand its
 615 distribution. *Parus major*, *Regulus ignicapillus* and
 616 *Sylvia atricapilla*, associated with woodlands (Cramp
 617 and Perrins 1993), were present in the initial woodland
 618 patches and their respective distributions became more
 619 continuous as woodland patches merged due to wood-
 620 land expansion. Finally, species such as *Certhia*
 621 *brachydactyla*, *Columba palumbus* and *Parus caeruleus*,
 622 which require bigger or more mature trees for
 623 nesting and/or feeding (Cramp and Perrins 1993),
 624 colonized new favourable patches that progressively
 625 appeared as woodlands matured. Our study suggests
 626 that, at the landscape scale, the temporal dynamics of
 627 the spatial distribution of increasing species are mainly
 628 controlled by the patterns of expansion of their
 629 preferred habitats. Contrary to the regional scale where
 630 metapopulation processes control the patterns of
 631 expansion (Wilson et al. 2004; Brotons et al. 2005)
 632 dispersal constraints are unlikely to occur at the
 633 landscape scale (Paradis et al. 1998).

634 Decrease in species occurrence was associated
 635 with distribution contractions (illustrated in Fig. 1).
 636 All declining species were already in the last stage of
 637 habitat loss: the contraction of existing occupied
 638 polygons (Hanski 1999) resulting from the loss of
 639 open habitats (Sirami et al. 2007). This study suggests
 640 that the distribution patterns of declining species
 641 result from the retractions in range following con-
 642 traction of optimal habitats (Johnson 1998). This
 643 result had also been found at the regional (Wilson

et al. 2004) scale, suggesting that declining species
 follow the same processes at both scales.

644 Stability in species occurrence was associated with
 645 diverse spatial dynamics of their distributions. Only
 646 four of the 16 stable species kept a constant
 647 distribution pattern through time. In this study, seven
 648 species showed fragmentation or contraction of their
 649 distribution although the change was not significant.
 650 This result is consistent with their ecological require-
 651 ments (species associated with shrubland and open
 652 habitat, negative or low scores on axis 1 of the co-
 653 inertia; Table 2) and suggests that these species are
 654 likely to undergo a future decrease in occurrence if
 655 the landscape becomes more forested.
 656
 657

Landscape factors behind distribution dynamics 658

659 Most species appeared to respond significantly to
 660 changes in land cover patterns at the landscape scale.
 661 Over the decades considered, the spatial distribution
 662 of most species showed little persistence and this was
 663 correlated to vegetation change. The persistence or
 664 non-persistence of a given part of the species range
 665 (polygon) was significantly explained by this poly-
 666 gon's vegetation composition. Although some of the
 667 differences in vegetation cover were small, they were
 668 all consistent with the past land cover dynamics and
 669 species habitat requirements. In the context of
 670 abandonment and landscape closure, wooded habitats
 671 were either stable or expanding (Sirami et al. 2007).
 672 Thus, woodland-associated bird species tended to
 673 increase in occurrence and to expand their distribu-
 674 tion. In addition, once they were present in a location,
 675 they tended to continue to be observed there. The low

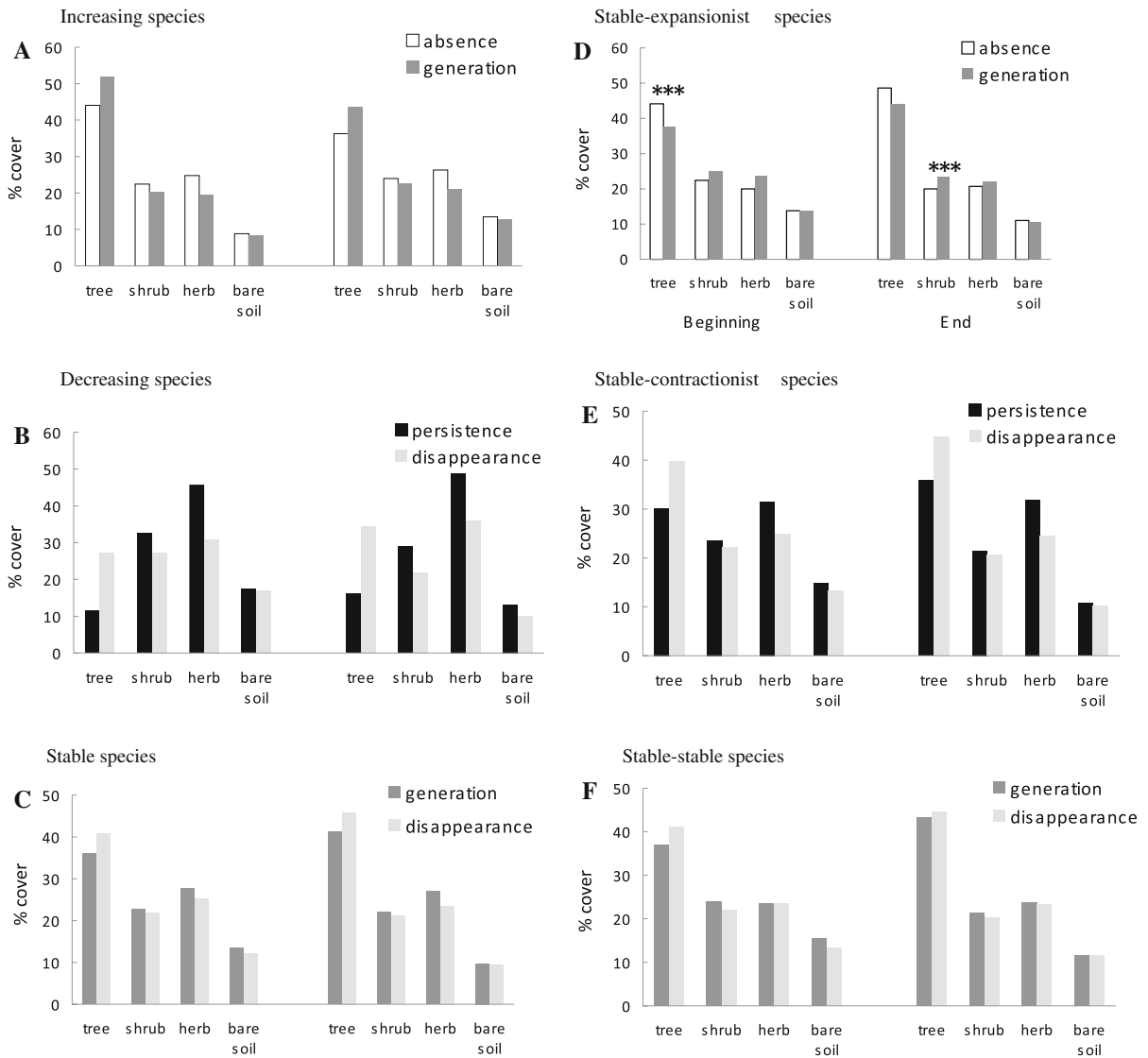


Fig. 5 Comparison of vegetation cover (tree, shrub, her, bare soil) at the beginning and end of the time interval considered (1978–1992, 1992–2003 or 1978–2003) for contrasting types of polygons: **a** Increasing species; **b** Decreasing species;

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

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

696 potentially favourable polygons (Maron et al. 2005).
 697 The lower percentage of persistence of the distribu-
 698 tion of specialist species may be explained by a
 699 higher proportion of specialist species associated with
 700 transitory habitats such as heterogeneous shrubland
 701 (e.g. *Sylvia melanocephala*, Fig. 4c).

702 Lessons for conservation

703 All the decreasing species in our study were already
 704 showing marked population fragmentation at the onset
 705 of our long term study and were experiencing the last
 706 stage of habitat loss. This suggests that fragmentation
 707 of distribution at the landscape scale occurs early in the
 708 process of species decline and that taking spatial
 709 dynamics of species distribution into account in a
 710 context of land use changes could allow better and
 711 earlier assessment of species vulnerability. As vegeta-
 712 tion was not taken into account in the methods we used
 713 to obtain species distribution, our study is likely to
 714 underestimate fragmentation due to the presence of
 715 unsuitable habitat within the predicted species distri-
 716 bution. As a result, this emphasizes the endangered
 717 status of the five declining species studied in this paper
 718 (*Emberiza hortulana*; *Lanius senator*; *Serinus serinus*;
 719 *Sylvia undata*; *Carduelis chloris*) as fragmentation of
 720 the remaining open habitats will facilitate the estab-
 721 lishment and growth of woody species (Debussche and
 722 Lepart 1992) and further increase the risk of local
 723 extinction within these remaining patches. Our results
 724 also suggest that studying the spatial structure of
 725 species distribution patterns may provide information
 726 about population dynamics not only at the regional
 727 (Wilson et al. 2004) but also at the landscape scale.
 728 Spatial analyses also showed that, contrary to the
 729 trends of their occurrence rates, species considered
 730 stable were highly and potentially negatively affected
 731 by land use changes. As a result they could be
 732 experiencing the early stages of population decline
 733 and should be included in management policies. Thus
 734 proper knowledge of temporal changes in distribution
 735 may help predict species vulnerability even in the
 736 absence of solid data on numerical trends.

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References

- Bibby CJ, Burgess ND, Hill DA (1992) Bird census techniques. Cambridge University Press, Cambridge
- Brotons L, Pons P, Herrando S (2005) Colonization of dynamic Mediterranean landscapes: where do birds come from after fire? *J Biogeogr* 32:789–798. doi:10.1111/j.1365-2699.2004.01195.x
- Burel F, Butet A, Delettre YR, de la Pena NM (2004) Differential response of selected taxa to landscape context and agricultural intensification. *Landsc Urban Plan* 67:195–204. doi:10.1016/S0169-2046(03)00039-2
- Burrough P, McDonnell R (1998) Principles of geographical information systems. Oxford University Press, New York
- Carr JR, Roberts KP (1989) Application of universal kriging for estimation of earthquake ground motion: statistical significance of results. *Math J* 21:255–265
- Chamberlain DE, Fuller RJ (2000) Local extinctions and changes in species richness of lowland farmland birds in England and Wales in relation to recent changes in agricultural land-use. *Agric Ecosyst Environ* 78:1–17. doi:10.1016/S0167-8809(99)00105-X
- Cramp S, Perrins CM (1993) Handbook of the Birds of Europe, the Middle East and North Africa: the birds of the western Palearctic. Oxford University Press, Oxford
- Debussche M, Lepart J (1992) Establishment of woody plants in mediterranean old fields: opportunity in space and time. *Landscape Ecol* 6:133–145. doi:10.1007/BF00130026
- Debussche M, Rambal S, Lepart J (1987) Les changements de l’occupation des terres en région méditerranéenne humide: évaluation des conséquences hydrologiques. *Acta Oecol* 8:317–332
- Farina A (1995) Distribution and dynamics of birds in a rural sub-Mediterranean landscape. *Landsc Urban Plan* 31:269–280. doi:10.1016/0169-2046(94)01052-A
- Gonzalo-Turpin H, Sirami C, Brotons L, Gonzalo L, Martin J-L (2008) Teasing out biological effects and sampling artefacts when using occupancy rate in monitoring programs. *J Field Ornithol* (in press)
- Hanley JA, McNeil BJ (1982) The meaning and use of the area under a receiver operating characteristic (ROC) curve. *Radiology* 143:29–36
- Hanski I (1999) Metapopulation ecology. Oxford Univ. Press, Oxford
- Johnson CN (1998) Species extinction and the relationships between distribution and abundance. *Nature* 394:272–274. doi:10.1038/28385
- Johnston K, Ver Hoef JM, Krivoruchko K, Lucas N (2001) Using ArcGIS geostatistical analyst. GIS by ESRI, Redlands, California

- 800 Lavergne S, Thuiller W, Molina J, Debussche M (2005) 831
 801 Environmental and human factors influencing rare plant 832
 802 local occurrence, extinction and persistence: a 115-year 833
 803 study in the Mediterranean region. *J Biogeogr* 32:799– 834
 804 811. doi:10.1111/j.1365-2699.2005.01207.x 835
 805 Legendre P, Fortin M-J (1989) Spatial pattern and ecological 836
 806 analysis. *Vegetatio* 80:107–138. doi:10.1007/BF00048036 837
 807 Litvaitis JA (1993) Response of early-successional vertebrates 838
 808 to historic changes in land use. *Conserv Biol* 7:866–873. 839
 809 doi:10.1046/j.1523-1739.1993.740866.x 840
 810 MacKenzie DI, Nichols JD, Lachman GB, Droege S, Royle JA, 841
 811 Langtimm CA (2002) Estimating site occupancy rates 842
 812 when detection probabilities are less than one. *Ecology* 843
 813 83:2248–2255 844
 814 Maron M, Lill A, Watson DM, Mac Nally R (2005) Temporal 845
 815 variation in bird assemblages: how representative is a one- 846
 816 year snapshot? *Austral Ecol* 30:383–394. doi:10.1111/j. 847
 817 1442-9993.2005.01480.x 848
 818 Maruca SL, Jacquez GM (2002) Area-based tests for associa- 849
 819 tion between spatial patterns. *J Geogr Syst* 4:69–84. doi: 850
 820 10.1007/s101090100075 851
 821 Moreira F, Beja P, Morgado R, Reino L, Gordinho L, Delgado 852
 822 A, Borralho R (2005) Effects of field management and 853
 823 landscape context on grassland wintering birds in South- 854
 824 ern Portugal. *Agric Ecosyst Environ* 109:59–74. doi: 855
 825 10.1016/j.agee.2005.02.011 856
 826 Paradis E, Baillie SR, Sutherland WJ, Gregory RD (1998) 857
 827 Patterns of natal and breeding dispersal in birds. *J Anim* 858
 828 *Ecol* 67:518–536. doi:10.1046/j.1365-2656.1998.00215.x 859
 829 Preiss E, Martin JL, Debussche M (1997) Rural depopulation 860
 830 and recent landscape changes in a Mediterranean region: 861
 consequences to the breeding avifauna. *Landscape Ecol* 831
 12:51–61. doi:10.1007/BF02698207 832
 R Development Core Team (2008) R: a language and envi- 833
 ronment for statistical computing. R Foundation for Sta- 834
 tistical Computing, Vienna, Austria 835
 Sadahiro Y, Umermura M (2000) Spatio-temporal analysis of 836
 polygon distributions: event-based approach. CSIS Dis- 837
 cussion Paper Series No. 25, Center for Spatial Informa- 838
 tion Science, University of Tokyo, Japan 839
 Sirami C, Brotons L, Martin JL (2007) Vegetation and song- 840
 bird response to land abandonment: from landscape to 841
 census-plot. *Divers Distrib* 13:42–52 842
 Sirami C, Brotons L, Burfield I, Fonderflick J, Martin J-L 843
 (2008) Is land abandonment having an impact on biodi- 844
 versity? A meta-analytical approach to bird distribution 845
 changes in the north-western Mediterranean. *Biol Conserv* 846
 141:450–459. doi:10.1016/j.biocon.2007.10.015 847
 Suarez-Seoane S, Osborne PE, Baudry J (2002) Responses of 848
 birds of different biogeographic origins and habitat 849
 requirements to agricultural land abandonment in northern 850
 Spain. *Biol Conserv* 105:333–344. doi:10.1016/S0006- 851
 3207(01)00213-0 852
 Thomas CD, Bulman CR, Wilson RJ (2008) Where within a 853
 geographical range do species survive best? A matter of 854
 scale. *Insect Conserv Divers* 1:2–8. doi:10.1111/j.1752- 855
 4598.2007.00001.x 856
 Wilson RJ, Thomas CD, Fox R, Roy DB, Kunin WE (2004) 857
 Spatial patterns in species distributions reveal biodiversity 858
 change. *Nature* 432:393–396. doi:10.1038/nature03031 859
 860

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