BIODIVERSITY RESEARCH

Vegetation and songbird response to land abandonment: from landscape to census plot

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ABSTRACT

While intensification of human activities and its ecological effects in many natural areas have recently received much attention, land abandonment in marginal areas is still the largely ignored side of a process rooted in the same socioeconomic context. Decreasing human impact in marginal rural areas often triggers a recovery of seminatural vegetation. Over a period of 25 years, we studied the changes in landscape and vegetation structure that followed land abandonment in a traditional Mediterranean mosaic of crops, grasslands, shrublands and woodlands, and assessed their effects on songbird occurrence and distribution. We combined an analysis of vegetation changes based on aerial photo interpretation with an analysis of bird censuses from 1978, 1992 and 2003 at two spatial scales: landscape and census plot (respectively 2800 and 3 ha). The perceived temporal changes in the vegetation were scale dependent. At the landscape scale, open habitats tended to disappear and woodlands matured. The contrasts in vegetation structure that defined habitat patches at the onset of the study tended to disappear. There was an overall shift of the bird community in favour of woodland species. At the scale of the census plot, however, the colonization by woody vegetation of patches formerly characterized by a homogeneous grass cover increased the local diversity of the vegetation, at least temporarily. Of seven species dependent on open habitats, the occurrence rate of five species significantly decreased, whereas it increased for two species: woodlark (*Lulula arborea*) and melodious warbler (*Hippolais polyglotta*). This increase was linked to the transitional increase in local vegetation diversity. In patches originally dominated by woodlands, local vegetation diversity decreased as woody vegetation expanded into clearings. The occurrence rate significantly increased for seven species relying on closed woodlands, while it decreased for two woodland species. As most species of high conservation profile in the Mediterranean are tied to open or to heterogeneous transitional habitats, these trends raise questions concerning their persistence in the future.

Keywords

Bird, Mediterranean, land abandonment, landscape, scale.

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INTRODUCTION

Current land use changes negatively affect biodiversity and are one of the main components of global change (Vitousek *et al.*, 1997). Since the middle of the 20th century, a growing demand for higher economical productivity has prompted two contrasting processes: land use intensification in areas most favourable to agriculture, and land abandonment in areas where agriculture was considered uneconomical (Bouma *et al.*, 1998). Abandonment is widespread in several regions of North America (Parody *et al.*, 2001), as well as of Eastern (Robinson & Sutherland, 2002) and Southern Europe (Ostermann, 1998). While intensification involves profound shifts in land management that threaten biodiversity (Stoate *et al.*, 2001; Burel *et al.*, 2004), abandonment, in contrast, leads to a relaxation of human-caused disturbance and favours natural vegetation dynamics (Debussche *et al.*, 1987). The closing of the parts of the landscape that were maintained open by grazing or agriculture and the cessation of traditional wood extraction for firewood or charcoal (Debussche *et al.*, 1999; Romero-Calcerrada & Perry, 2004) are expected to cause a progressive reduction in contrast between the patches that defined the initial landscape mosaic. But, beyond these predictable, coarse-grained changes in landscape physiognomy, fine-grained changes are also expected at the scale of individual land cover

patches. In particular, the initially simple one layer structure of the open habitat patches that resulted from agriculture or intensive grazing should change into a complex multilayer structure because of their progressive colonization by shrubs. These fine-grained patchworks of shrubs and grassy patches should be transitory and transform into closed shrublands and, ultimately, into closed woodlands. Although one expects that such changes should influence animal distribution and population dynamics (Wiens, 1989), our knowledge about the actual effects of land abandonment on animal communities remains scant (but see Russo, 2004). Which species from the initial species pool will benefit, suffer or remain unaffected by these changes and why? Will new species colonize the new landscape? How will species respond to broad-scale landscape simplification and to local-scale changes in habitat structural complexity?

To address these questions, we combined data on long-term changes in faunal distribution with information on temporal changes in vegetation extracted from aerial photographs. To describe changes in vegetation, we analysed temporal changes in distribution of land cover types at the landscape scale and those in proportion of vegetation classes at the census-plot scale. We selected a study area in the Mediterranean region of southern France that had been subject to land abandonment since the middle of the 20th century and where songbird distribution had been recorded at three points in time over a period of 25 years. The present work is a temporal and methodological extension of an earlier study (Preiss et al., 1997).

We addressed two spatially explicit questions: (i) How did the proportion of the land cover types and the occurrence rates of songbirds change with time at the landscape scale? (ii) How did vegetation structure and songbird communities change with time at the scale of the census plot within each initial land cover type?

METHODS

Study area

The study area was situated 20 km north of Montpellier (southern France) (43°47′ N, 03°50′ E). It covers 2800 ha and includes a karstic limestone plateau, marly hills and plains, and cliffs. Altitude ranges from 125 m to 658 m at the Pic Saint Loup. The climate is Mediterranean, with moist and cold winters. The annual average rainfall ranges from 950 mm to 1350 mm, average maximum temperature during the warmest month is 28 °C and average minimum temperature during the coldest month is −1 °C (Debussche & Escarre, 1983).

Until the middle of the 20th century grasslands were extensive in the study area. The shrublands were used for grazing sheep (meat production) and for the production of juniper oil. The oak woodlands were coppiced at 30-year intervals for charcoal (Debussche et al., 1987). The last peak of intensive use occurred during World War II in response to the need to produce meat (mutton) and charcoal for the inhabitants of the nearby city of Montpellier. Around the 1960s, land abandonment was accentuated by the strengthening of the market forces as well as social

changes. Between the 1960s and the 1980s, the proportion of the study area used for grazing went from 90% to less than 30%. In the areas still grazed, sheep density decreased from 1 sheep/ha to 0.25 sheep/ha (Larinier, 2003). After the 1980s, new land uses appeared on limited areas (350 ha): bull and horse grazing in enclosures, quality vineyards on slopes, and 'village' sprawl around existing settlements (Larinier, 2003).

Bird community sampling

We used the 194 census plots defined in 1978 (Preiss et al., 1997; Fig. 1). The bird community was surveyed by 20-min point counts with unlimited distance (Bibby et al., 1992) in 1978, 1992 and 2003. As we did observe over 50% of the birds recorded within 50 m from the observer, we estimated that most of the birds recorded were located within 100 m from the centre of the census plot, and therefore considered that a census plot covered an area of about 3 ha. Plots were censused once each year, with a random order in 1978, then with the same order in 1992 and 2003. Birds were counted by J.L. Martin in 1978, E. Preiss in 1992 and C. Sirami in 2003. Censuses took place during the breeding season (March–June). They were restricted to days without marked rainfall or wind and during the period of peak vocal activity (4 h after sunrise). Raptors, aerial feeders (swallows, swifts and bee-eaters) and crepuscular species were excluded from the analysis because the point-count method is not appropriate to assess their abundance (Bibby et al., 1992). Rare species were excluded from the analyses. As a result, we only considered species present in at least two of the three years and at more than 10 plots within one year (34 species). We used uncorrected presence–absence. Turpin (2003) had shown, using the PRESENCE software (MacKenzie et al., 2002), that detectability biases caused by observer (confounded with year), wind velocity, cloud cover, date and sampling hour did not significantly affect occupancy rate estimations in our data set when 20-min-long censuses were used.

Definition of landscape and census-plot scales

We defined the landscape scale as the whole study area (2800 ha), in which we studied changes in the spatial extent of the five natural and two human-made land cover types identified in the study area. We used the census plots as a local scale (3 ha) at which to analyse the temporal changes in the proportion of pixels (pixel size = 0.7 m) associated with four main vegetation classes and the changes in the composition of the bird community. We restricted this local-scale analysis to the census plots located in the natural land cover types.

Landscape-scale analysis

We used land cover maps to analyse temporal changes in the total extent of the land cover types. We used infrared aerial photographs taken in years 1981, 1992 and 2002, the closest possible to the years when birds had been censused (1978, 1992 and 2003). Photographs were ortho-rectified and geo-referenced to Lambert Conformal Conic system with a spatial resolution of
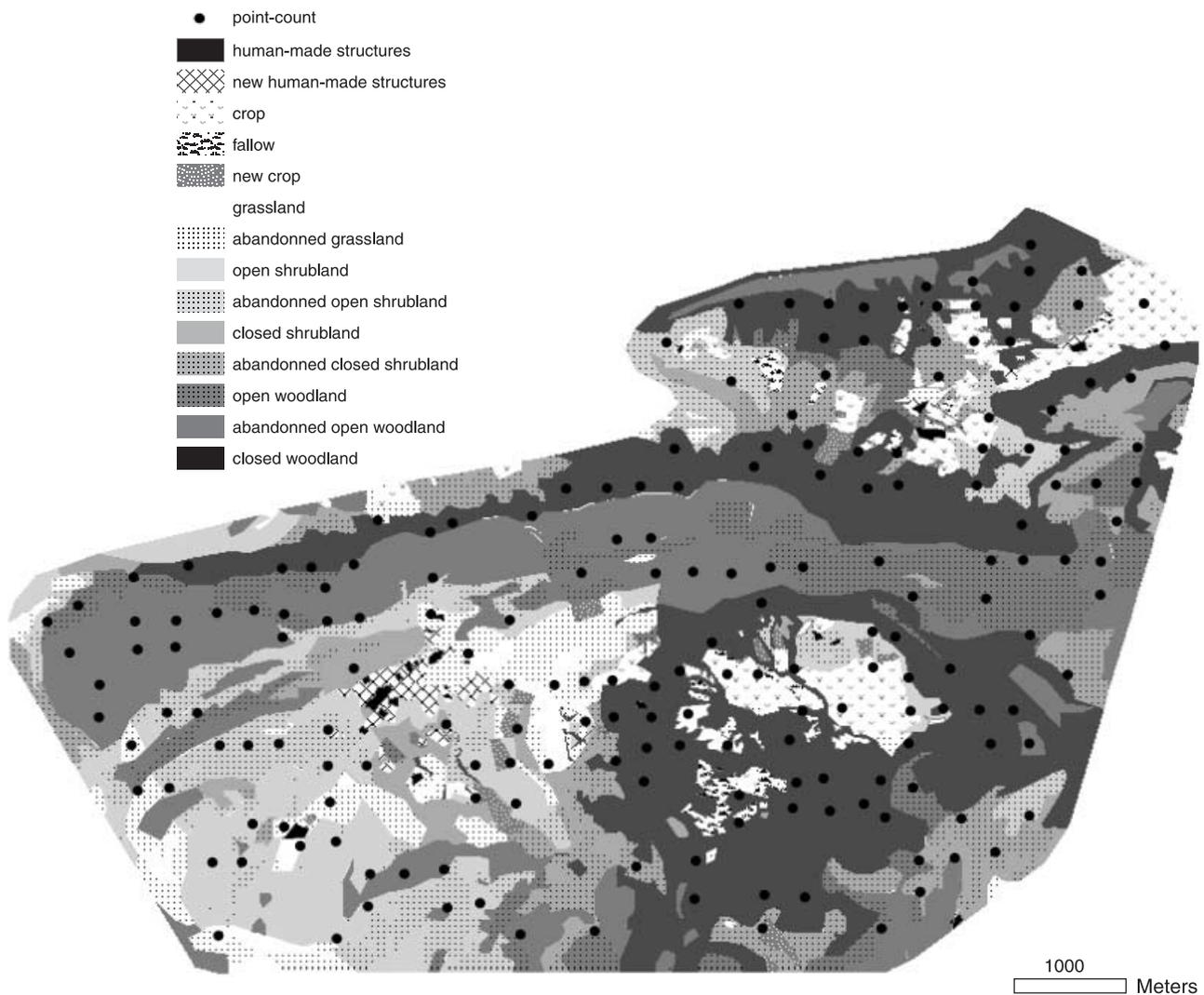
Figure 1 Map of the study area with the location of the 194 point counts and the main vegetation changes between 1981 and 2002. We mapped the seven land cover types that persist over the period 1981–2002 as well as seven transition categories corresponding to polygons that moved from one category to another: new human-made structures = from any land-cover type to human made structures; fallow = from crop to any land-cover type; new crop = from any land-cover type to crop; abandoned grassland = from grassland to any land-cover type further in the succession. Marginal transitions were not mapped.

0.7 m in ENVI 4.0 (RSI Research Systems, 1996). We used ArcGIS 8.3 (Environmental Systems Research Institute, Inc.) complemented by field observation to obtain land cover maps for each year. We identified land cover polygons (minimum polygon size was approximately 0.05 ha, average polygon size = 2 ha) on the aerial photographs of the three years. We assigned these polygons to seven land cover types. Five land cover types consisted of spontaneous vegetation: grassland (grasses with other annuals and few short shrubs dominated by *Brachypodium retusum* (Pers.) P. Beauv. or *Bromus erectus* Hudson); open shrubland (shrubs ranging from 0.5 m to 2.5 m in height with a grass/bare ground cover higher than 30%, dominated by *Juniperus oxycedrus* L., *Buxus sempervirens* L. and *Rosmarinus officinalis* L.); closed shrubland (associations of shrubs and of scattered trees, representing a total cover of more than 30%, dominated by

J. oxycedrus, *B. sempervirens* and *R. officinalis*); open woodland (trees taller than 3 m with a grass/bare ground cover higher than 30%, dominated by *Quercus ilex* L., *Pinus halepensis* Miller or *Quercus pubescens* Willd.), and closed woodland (dense trees taller than 3 m with few shrubs and less than 30% covered by grass/bare ground, dominated by *Q. ilex*, *P. halepensis* or *Q. pubescens*). Two land cover types consisted of human-made habitats: human-made structures (clustered or isolated buildings and associated gardens) and crops (1–2 ha plots of wine grapes, cereals or olive trees). We cross-tabulated land cover maps in order to obtain a transition matrix (Table 3) that allowed quantifying the spatial extent that had been lost or gained by a given land cover type over the entire study period (from 1981 to 2002). We constructed a synthetic map showing the main vegetation changes between 1981 and 2002.

We used Generalized Estimating Equations (GEE, SAS version 8; SAS Institute Inc., 1999) to investigate temporal changes in overall occurrence rates of individual bird species in the study area between years. GEE are an extension of generalized linear models for correlated data which are suited for binary repeated data (Lipsitz *et al.*, 1994). We analysed these changes between each pair of years. To be conservative, we only considered significant changes associated with *P*-values smaller than 0.01. Species that changed significantly in occurrence rate between 1978 and 2003 were considered decreasing or increasing if trends were consistent during the two subperiods. 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 also did not show significant opposite trends during the two intermediate periods (1978–1992, 1992–2002) were considered stable. We compared these trends with the national trends obtained from the French Breeding Bird Survey (FBBS; http://www.mnhn.fr/mnhn/crbpo/résultats_etat_populations.htm#resultat), except for four species for which the FBBS provided no trends and for which we used the European Bird Database (Birdlife International, 2004) (Table 4).

Census-plot analysis

We restricted this analysis to the 184 census plots located in the natural land cover types (excluding crops and human-made structures, marginal in the landscape; average polygon size for natural land cover types = 4.8 ha). We used a pixel classification of the three aerial photographs (pixel size = 0.7 × 0.7 m) to quantify fine-grained vegetation changes at the scale of the census plot. We identified four pixel classes: Bare Ground (little or no vegetation), Herb (herbaceous vegetation), Shrub (woody vegetation 0.5–2.5 m) and Tree (woody vegetation > 3 m). We used a maximum-likelihood supervised method (Campbell, 1996) in ENVI to assign each pixel in the study area to one of the four pixel classes on each of the three photographs. We tested the accuracy of classifications for each of the three years with a confusion matrix comparing ground-truthed pixel classification to photographic-based pixel classification for a test data set (around 5000 pixels). The overall accuracy remained constant over the years (kappa coefficient were, respectively, 0.84, 0.82 and 0.83 for 1981, 1992 and 2002) for all pixel classes (Table 1), which legitimated the study of vegetation changes across years by analysing changes in the proportion and distribution of these four classes of pixels from one year to another. We calculated for each year the proportion of the four pixel classes for each census plot (within 100 m of the centre of the census plot, about 3 ha).

We used a co-inertia analysis (Doledec & Chessel, 1994; R Software, R Development Core Team, 2004) to analyse temporal changes in vegetation composition and bird communities at the census-plot scale. The co-inertia analysis is particularly suited for the simultaneous detection of faunal and environmental features in studies of ecosystem structure because the resulting sample

Table 1 Confusion matrices for the classification of the aerial photograph. Each row indicates the proportion (%) of the pixels that have been correctly assigned to the class of vegetation directly observed on the ground and the proportion and nature of the incorrect assignments

		Classification value			
	Ground value	Tree	Shrub	Herb	Bare Ground
1981	Tree	93.66	5.54	0.8	0
	Shrub	15.83	76.26	7.23	0.68
	Herb	0	5.2	84.89	9.91
	Bare Ground	0	0	7.11	92.89
1992	Tree	93.5	4.18	2.3	0
	Shrub	14.74	68.63	16.53	0.1
	Herb	0.88	5.7	90.77	2.65
	Bare Ground	0.7	2.5	7.28	89.52
2002	Tree	82.91	14.20	2.9	0
	Shrub	10.35	69.35	19.7	0.6
	Herb	0	1.29	97.91	0.8
	Bare Ground	0	0.2	0.1	99.7

scores (environmental scores and faunal scores) are the most covariant (Doledec & Chessel, 1994), especially when the variables are correlated (Dray *et al.*, 2003). It provides an ordination of census plots based on the environmental variable co-inertia weights and one based on the bird species co-inertia weights. The bird assemblage data set consisted of 34 bird species presence/absence for the 552 censuses (184 census plots × 3 years) and the vegetation data set consisted of four pixel classes cover for the same 552 censuses. We estimated the significance of the temporal variation over the whole study period considering the 184 census plot scores for each ordination with a Wilcoxon signed rank test (STATISTICA 6.1; StatSoft France, 2003). Census plots were assigned to one of the five natural land cover types identified for that location in 1981. For each initial land cover type we plotted the 1981, 1992 and 2002 average vegetation scores of the census plots and the 1978, 1992 and 2003 average faunal scores of the census plots on axis 1 and axis 2 of the co-inertia analysis (Fig. 2a,b). Finally, to look at correlations between songbird distribution and vegetation composition, we plotted bird species scores and vegetation vectors, showing the correlation of the four vegetation pixel classes with the axes, on the axis 1 × axis 2 co-inertia plane (Fig. 2c).

We used the Shannon Diversity Index to study temporal changes in vegetation diversity within census plots between 1981 and 2002 (Shannon Diversity Index, $SHDI = -\sum_{i=1}^{m}(P_i \ln P_i)$ with m the number of pixel classes (four) and P_i the proportion of area covered by pixel class (i). We compared changes in the cover of the four pixel classes and changes in $SHDI$, first for the 184 census plots, and then for the subsets of census plots assigned to each of the five initial land cover types in 1981. We estimated the significance of the temporal changes with Wilcoxon signed rank tests.
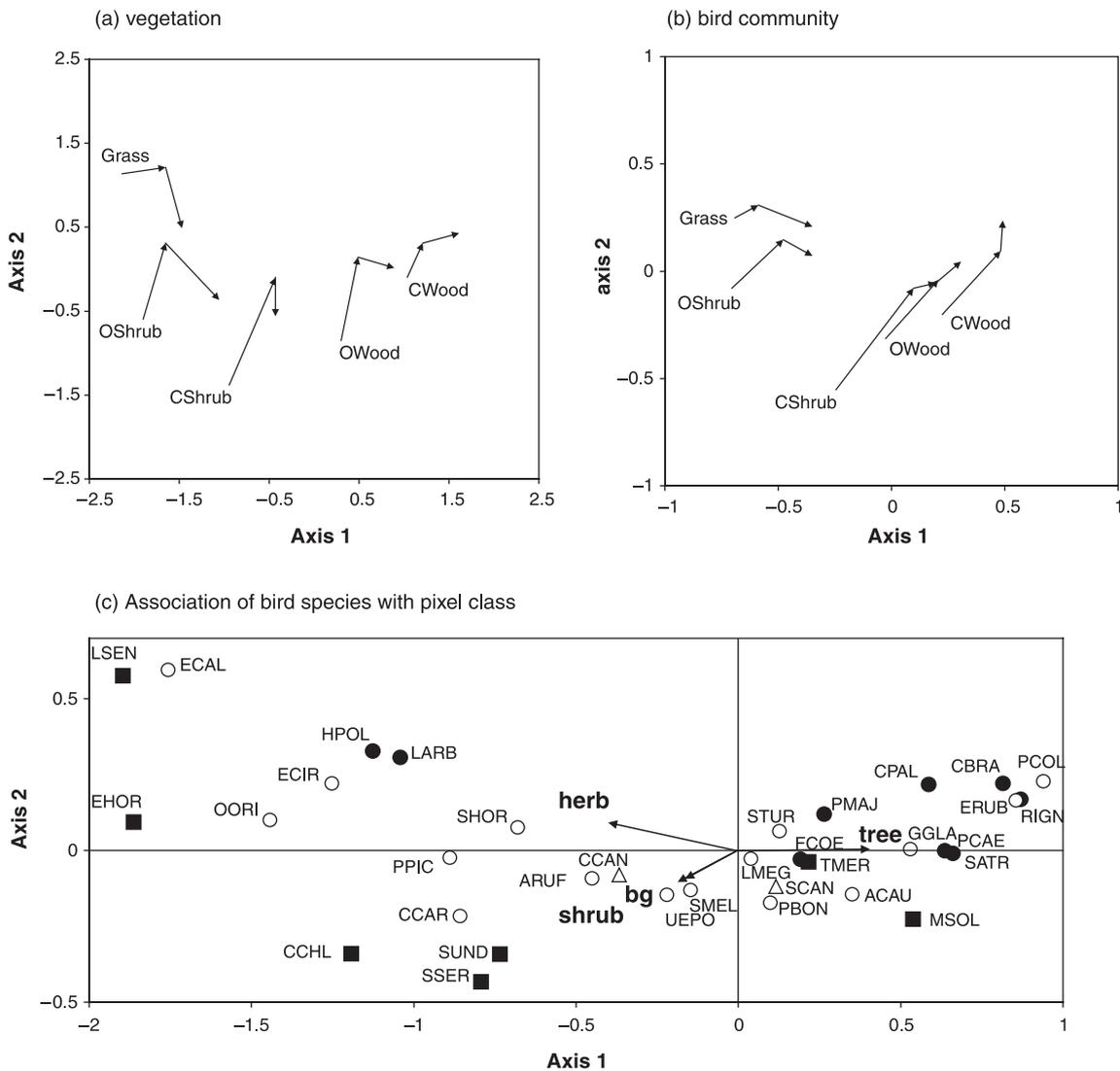
(a) vegetation

(b) bird community

(c) Association of bird species with pixel class

Figure 2 Axis 1 and axis 2 plane of co-inertia analysis showing temporal shifts in vegetation composition, songbird community composition and the relationships between pixel classes (vegetation variables) and songbirds. (a) Temporal shifts in position of census plots on axis 1 × axis 2 co-inertia plane, using environmental variable (the four pixel classes describing the vegetation) co-inertia weights (scores of census plots were averaged within each subset of plots assigned to a given land cover type in 1981); the base of the arrows represents the average scores of a sample in 1981 or in 1992 and its heads the average scores in 1992 or in 2002, respectively; each arrow is identified by the acronym of the land cover type these plots had been assigned to in 1981); (b) temporal shifts in position of census plots on axis 1 × axis 2 co-inertia plane, using bird species co-inertia weights (scores of census plots were averaged within each samples as for the analysis of the vegetation); (c) scores of bird species and of pixel classes on axis 1 × axis 2 co-inertia plane (bird species acronyms are defined in Table 2, bird species symbol refer to species with decreasing (■), increasing (●), stable (○), or non-consistent (△) occurrence changes during the period considered in the GEE analysis (bg refers to 'bare ground').

RESULTS

Landscape-scale analysis

The analysis of temporal changes in the total extent of the land cover types showed that substantial land cover changes occurred at the landscape scale from 1981 to 2002. The spatial extent of grassland decreased by 64%, that of open shrubland by 21% and that of closed shrubland by 41% (Table 2, Fig. 1). The spatial extent of closed woodland increased by 45%. The spatial extent

of open woodland remained constant over the period. As a result, 14% of the study area initially within the open land cover types had been lost, while 13% of the study area had been converted into closed woodland (Table 2). Human-made structures and crops remained marginal in the landscape although human-made structures increased by more than 300%. Over one-third of the study area had undergone a land cover transition (Table 3). Between 1981 and 2002, 71.6% of the spatial extent initially classified as grassland changed, mainly into open shrubland. Half of the initial open shrubland had changed into closed shrubland or

Table 2 Extent of the seven land cover types in 1981, 1992 and 2002 (measured in percentage of the study area) and temporal changes in cover between 1981 and 2002 (measured in percentage of the study area and in percentage of their initial extent in 1981)

	1981	1992	2002	1981–2002 Percentage study area	1981–2002 Percentage initial extent
Human-made structures (Built)	0.3	0.5	1.2	1.0	331.7
Crop	4.9	4.5	5.6	0.7	13.6
Grassland (Grass)	7.9	3.8	2.9	−5.0	−63.9
Open shrubland (OShrub)	17.3	17.6	13.7	−3.6	−20.8
Closed shrubland (CShrub)	14.1	10.6	8.3	−5.8	−40.9
Open woodland (OWood)	25.7	22.0	25.0	−0.6	−2.5
Closed woodland (CWood)	29.8	41.0	43.2	13.4	45.0

Table 3 Matrix showing changes in the extent of land cover types between 1981 and 2002 over the entire study area. Each row indicates the proportion (%) of the pixels with a given land cover type at the beginning of the study period (1981) that transformed into the different land cover types at the end of the period (2002). For definition of acronyms see row one of Table 2

2002 / 1981	Built	Crop	Grass	OShrub	CShrub	OWood	CWood	Initial habitat affected (%)	Study area affected (%)
Built	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Crop	0.0	78.7	3.0	11.7	1.8	1.1	3.7	21.3	1.0
Grass	2.8	9.0	28.4	46.6	5.2	6.7	1.3	71.6	5.7
OShrub	2.6	1.9	2.1	49.0	17.4	23.2	3.8	51.0	8.8
CShrub	1.6	2.5	3.2	0.0	32.6	28.9	31.2	67.4	9.5
OWood	0.0	0.1	0.0	1.5	0.6	63.1	34.7	36.9	9.5
CWood	0.2	1.0	0.0	0.8	0.2	0.5	97.3	2.7	0.8
Total									35.3

open woodland. Two-thirds of the spatial extent initially classified as shrubland had become open or closed woodland while one-third of open woodland became closed woodland (Table 3).

The analysis of temporal changes in the occurrence rate of bird species at the landscape scale showed that the occurrence of 16 bird species changed between 1978 and 2003: nine increased and seven decreased significantly and consistently over the two periods (Table 4). One species (the wood pigeon, *Columba palumbus*) absent from the census in the first year had become common in the last year. Among the species that decreased, two (*Emberiza hortulana* and *Monticola solitarius*) were present, respectively, in 20 and 13 census plots during the first year of study, but were not observed during the last year of study. Within the 18 species that did not show a significant difference in occurrence rate between 1978 and 2003, only two showed significant but opposite trends over the two intermediate periods. We considered the remaining 16 of these species as stable (Table 4) at the landscape scale.

Census-plot analysis

The co-inertia analysis of temporal changes in vegetation composition and bird communities at the census-plot scale showed a first axis identified as an avifauna and vegetation gradient going from open habitats (axis negatively correlated to variable Herb) and their associated bird species (negative scores) to forested lands (axis positively correlated to variable Tree) and their associated bird species (positive scores). The second axis defined a gradient going from census plots dominated by shrubs and their associated species (negative scores) to census plots dominated by grasses and their associated bird species (positive scores). Over the whole period studied, vegetation scores of the census plots significantly shifted towards higher scores along the axis from open to forested lands defined by axis 1 of the co-inertia analyses (Fig. 2a) (Wilcoxon signed rank test on axis 1 score for 1981 and 2002, $P < 0.05$). Moreover, scores converged with time towards null values along axis 2, which suggests a shift in the vegetation of the census plots towards vegetation with less bare ground and less shrubs (Wilcoxon signed rank test on axis 2 score for 1981 and 2002, $P < 0.05$, and on axis 2 absolute values for 1981 and 2002, $P < 0.05$). Bird community composition (Fig. 2b) shifted along axis 1 (Wilcoxon signed rank test on axis 1 scores for 1978 and 2003, $P < 0.05$) from communities with a higher proportion of species correlated with pixels associated with open habitats (variable Herb and to a lesser degree variables Bare Ground and Shrub) to communities with a higher proportion of species associated with pixels correlated to forested lands (Tree, Fig. 2c). Scores also shifted along axis 2 to converge (null values of axis 2) towards communities with a lower proportion of species correlated to pixel classes Herb, Bare Ground and Shrub (Fig. 2c) (Wilcoxon signed rank test on axis 2 score for 1978 and 2003, $P < 0.05$, and on axis 2 absolute values, $P < 0.05$). Two main

Table 4 Bird species ordered by occurrence change between 1978 and 2003

Occurrence change	Species	ACR	GEE	1978	1992	2003	FBBS
Significant decrease	*Emberiza hortulana*	EHOR	< 0.0001	20	10	0	−1*
	Monticola solitarius	MSOL	0.0004	13	2	0	ND*
	Lanius senator	LSEN	0.001	17	13	3	−1*
	Carduelis chloris	CCHL	< 0.0001	50	4	8	−1
	Serinus serinus	SSER	0.002	49	21	26	−1
	Sylvia undata	SUND	< 0.0001	76	23	18	F*
	Turdus merula	TMER	0.0005	178	160	154	0
Significant increase	*Columba palumbus*	CPAL	< 0.0001	0	23	42	0
	Certhia brachydactyla	CBRA	< 0.0001	4	11	41	0
	Hippolais polyglotta	HPOL	0.0002	6	44	28	0
	Regulus ignicapillus	RIGN	< 0.0001	9	64	99	0
	Parus caeruleus	PCAE	0.006	15	27	32	0
	Lullula arborea	LARB	< 0.0001	24	17	51	0
	Parus major	PMAJ	< 0.0001	67	104	108	0
	Sylvia atricapilla	SATR	< 0.0001	85	119	130	0
	Fringilla coelebs	FCOE	< 0.0001	146	172	194	0
Non-significant change	*Aegithalos caudatus*	ACAU	0.027	27	36	13	0
	Alectoris rufa	ARUF	0.264	56	64	47	0
	Carduelis carduelis	CCAR	0.157	20	8	28	0
	Emberiza calandra	ECAL	0.127	23	13	16	−1
	Emberiza cirlus	ECIR	0.639	36	45	33	+1
	Erithacus rubecula	ERUB	0.015	79	78	98	+1
	Garrulus glandarius	GGLA	0.17	30	43	21	0
	Luscinia megarhynchos	LMEG	0.024	171	163	155	0
	Oriolus oriolus	OORI	0.371	18	14	14	0
	Phylloscopus bonelli	PBON	0.105	27	15	17	−1
	Phylloscopus collybita	PCOL	0.346	9	5	13	0
	Pica pica	PPIC	0.433	18	27	15	−1
	Sylvia hortensis	SHOR	0.014	67	57	49	+1
	Sylvia melanocephala	SMEL	1	76	96	76	0
	Streptopelia turtur	STUR	0.608	86	74	81	0
	Upupa epops	UEPO	0.808	9	5	10	−1
Non-consistent change	*Cuculus canorus*	CCAN	0.642	69	44	66	−1
	Sylvia cantillans	SCAN	0.619	115	86	112	−1

ACR, acronyms; GEE, *P*-value for occurrence trend between 1978 and 2003 in GEE analysis; values, number of census plots in which the species were recorded in 1978, 1992 and 2003; FBBS, trends from the French Breeding Bird survey (except * = European Bird Database).
−1 = decreasing, 0 = stable, +1 = increasing, F = fluctuating, ND = unknown.

groups of species were identified on Fig. 1c: a tight cluster of species (positive scores on axis 1) with a strong correlation with pixel class Tree and a looser group of species (negative scores on axis 1) associated with census plots with shorter and more open vegetation either dominated by herbaceous vegetation (correlation to pixel class Herb and positive scores on axis 2) or with census plots characterized with open shrubby vegetation (pixel classes Shrub and Bare Ground, negative scores on axis 2). Species identified as decreasing in the previous section (Table 4) were mostly species associated with Herb or Bare Ground and Shrub, except *Turdus merula*, which was slightly correlated to pixel class Tree in the co-inertia analysis, and *M. solitarius*, which was linked to census plots with a high cover of both Trees and Bare Ground (Fig. 2c). Species that increased were closely correlated to Tree, except *Hypolais polyglotta* and *Lullula arborea*,

which were both associated with Herb. Species considered as stable at the landscape scale (Table 4) ranged widely in scores both along axis 1 and axis 2 of the co-inertia analysis.

The analysis of temporal changes in vegetation diversity within census plots showed that, in the 184 census plots considered, the average vegetation diversity within the census plots (SHDI) decreased during the study period as a result from a decrease in the number of pixels classified as Bare Ground or Shrub and an increase in the number of pixels classified as Tree (Table 5). When the initial land cover types were considered individually, the average vegetation diversity within the census plots of the initial grassland increased as a result of an increase in the number of pixels classified as Shrub and Tree and a reduction in the number of pixels classified as Bare Ground and Herb. Census plots from land cover types defined as Open and Closed Shrubland

Table 5 Temporal changes in pixel diversity (SHDI) and in cover of the 4 pixel classes between 1981 and 2002 in the 184 census plots as a whole and in the subsets of plots assigned in 1981 to each of the five land cover types with natural vegetation. *N*, number of census plots. For land cover type acronyms see Table 2. Significance of changes was tested by a Wilcoxon signed rank test with a *P* < 0.05 significance level: + refers to a significant increase, – refers to a significant decrease, NS refers to a non-significant change

	Study area	Grass	OShrub	CShrub	OWood	CWood
N	184	16	31	22	47	68
Shdi	–	+	ns	ns	–	–
Tree	+	+	+	+	+	+
Shrub	–	+	NS	–	+	–
Herb	NS	–	+	NS	–	+
Bare Ground	–	–	–	–	–	–

in 1981 did not change in vegetation diversity despite a decrease in the number of pixels classified as Bare Ground and Shrub and an increase in the number of pixels classified as Tree and Herb. In the census plots from land cover types initially defined as Closed Woodland, vegetation diversity decreased in response to a decrease in the number of pixels classified as Bare Ground and an increase in pixels classified as Tree.

DISCUSSION

Landscape simplification and local complexity

Thirty-five per cent of the study area had shifted in land cover types between 1981 and 2002. As remote sensing only allows describing the horizontal structure of the vegetation, it is likely that our results underestimate vegetation changes such as changes in understorey vertical structure or species composition in grassland. Our estimation of the extent of vegetation change in the study area should therefore be considered conservative. The co-inertia analysis has highlighted that the initial land cover types with natural vegetation had converged with time towards a more uniform landscape dominated by closed woodlands. Extensive grasslands had disappeared as they were colonized by shrubs and many shrublands had become woodlands. However, the analysis of the changes in the diversity of vegetation classes has identified contrasting trends at the local scale involving both simplification and increase in complexity. On the one hand, woodlands matured and lost small openings, leading to a more uniform forest land cover. On the other hand, the initial grassy stages of the vegetation succession, which were relatively homogeneous, transformed into more complex land cover with a fine grained juxtaposition of grassy patches and shrubs. In these particular patches one can hypothesize that, with time, shrub cover should increase, local vegetation diversity decrease, and a transition towards woodland take place. Said (2001) actually showed that such intermediate stages were restricted to a time window that ranged from 20 to 55 years after land abandonment. In most of our study area, sheep farming had stopped during the 1960s to the 1970s. Consequently, the shrublands that replaced them should have reached their maximum cover during the 1980s and 1990s, and should start changing into oak woodlands in the next decades, assuming the absence of major perturbation or of massive increases in wood demand in response to soaring fossil fuel prices.

Losers and winners

The occurrence rates of about 50% of the bird species had significantly changed between 1978 and 2003. The co-inertia analysis highlighted that bird assemblage of the initial land cover types converged towards assemblages of bird species associated with trees.

The pattern of change in species occurrence rates at the landscape scale over this 25-year period was consistent with the one described by Preiss *et al.* (1997) over the initial 14 years. Only *Cuculus canorus* and *Sylvia cantillans* did show inconsistencies in trends between the two periods. The explanation could rest in marked inter-annual variation in population size for these two species (C. S. pers. obs.). For declining species, trends were overall consistent with the FBBS (except *T. merula*, see below), indicating that similar processes are likely to occur at larger scales. For species with increasing occurrence rates, the FBBS indicated that all were stable at the national level, which could mean that, at larger scales, other processes compensate their increase in the Mediterranean region (e.g. fragmentation, Lauga & Joachim, 1992). The sharp decline in occurrence rate observed in 1992 for *M. solitarius* and *E. hortulana* were confirmed. The two species were entirely missing from the censuses in 2002. While *M. solitarius* was still present in several localities as shown by additional surveys, *E. hortulana* has to be considered as locally extinct as we failed to observe the species despite additional surveys designed to assess its presence. Finally, in 1978, a decade or more after the cessation of extensive grazing, two species typical of intensively grazed habitats, *Alauda arvensis* and *Anthus campestris*, were allready too rare to be taken into account in the analysis of community composition. The former has not been recorded after 1978, the latter is still present in 1992 and 2003 but rare.

Our analyses of the changes in the vegetation at the local census-plot scale suggest some underlying mechanisms that could link land cover changes, at both landscape and local levels, to trends in bird species occurrences. Most species that have decreased in occurrence rate were associated with census plots

that had a high proportion of pixels classified as Herb, Shrub or Bare Ground, and thus, to land cover types with open vegetation. These associations were consistent with what is known on the ecology of these species (Cramp & Perrins, 1993). However, two of the decreasing species (*T. merula* and *M. solitarius*) were associated with the woodland vegetation (co-inertia analysis) and their decrease in occurrence was inconsistent with the increase in proportion of woodlands in the landscape and in the proportion of pixel class Tree in the census plots. *Turdus merula* is identified in the literature as woodland or mixed woodland species (Cramp & Perrins, 1993) and the FBSS showed that this species was stable at the scale of France between 1989 and 2005 (cf. Table 4 as well as Jiguet & Julliard, 2006). As Camprodon & Brotons (2006) showed this species was not sensitive to changes in the under-storey, it is unlikely that local changes in the quality of forests, not measured by remote sensing, could be responsible for its decrease. An explanation for its slight but significant decline over the period 1978–2003 could be a long-term broad-scale population fluctuations starting before 1989. *M. solitarius* is a species linked to rocky outcrops and small cliffs (Cramp & Perrins, 1993). In our study area, these features are located on steep slopes and, thus, are surrounded by woodlands. The decrease in the amount of open patches within these habitats, where the species likes to feed on the ground (Yeatman-Berthelot & Jarry, 1994), might explain its trend.

Seven of the nine species that significantly increased in occurrence rate were linked to census plots with a high proportion of pixels classified as Tree. These species are all typical woodland and forest species (Cramp & Perrins, 1993). The two remaining species with increasing occurrence, *Lulula arborea* and *Hippolais polyglotta*, were exceptions: they were associated with pixel class Herb in the co-inertia analysis, association consistent with their description in the literature as species from heterogeneous open habitats (Cramp & Perrins, 1993). Change in distribution of these two species, counter-intuitive at first sight, can be understood when fine-grained changes in vegetation diversity are considered and especially the current fine-grained patchiness of the former grasslands. The hypothesis that an increase in local habitat structural complexity had a positive effect on these two species is consistent with the work from Pons *et al.* (2003) on *L. arborea* and with our own unpublished results on both species habitat selection by territory mapping. These results emphasize the need to complement studies on changes in habitat and on species distribution with studies on actual habitat use by birds (Law & Dickman, 1998).

'Stable' species

Most species that did not show significant trends in occurrence rate at the scale of the landscape were associated with the middle section of the vegetation gradient. Some of these species can be considered as woodland generalists (e.g. *Erithacus rubecula*; Cramp & Perrins, 1993). Others are more narrowly associated with transitional vegetation stages ('shrubland' species such as *Sylvia melanocephala*; Cramp & Perrins, 1993). Overall stability in occurrence rate at the landscape scale in such species can mask

different dynamics at a finer scale. In particular, it can mask spatial shifts in distribution that follow spatial shifts in the distribution of the land cover types they are associated with. In the case of species depending on shrublands, one can hypothesize that the colonization of grasslands by shrubs in the study area has compensated the transformation of former shrublands into woodlands. In the long term, however, if the current process of succession continues, such species may also decline and become rare or locally extinct.

Long-term trends?

Currently land abandonment has triggered a simplification of the traditional landscape mosaic (Farina, 1997). Under such circumstances a further increase of forest bird species and decrease of open habitat bird species seem inevitable in the northern Mediterranean Basin. As the decreasing species are often typical of the Mediterranean region (with often a high conservation status: *E. hortulana*, *Sylvia undata*, *Lanius senator*, *M. solitarius*) and as the increasing species are common Euro-Siberian species, northern Mediterranean bird communities will likely become more similar to Central European bird communities (Blondel & Farre, 1988). If this trend towards a simplification of the contrast between bird communities at the European scale shall be mitigated, the challenge for managers will be to find ways to maintain traditional Mediterranean habitat mosaics in which open habitats, local heterogeneity and woodlands would co-exist at any given point in time. This should also increase the diversity of other animals (Atauri & de Lucio, 2001) and help maintain biodiversity in the face of either intensification or land abandonment (Benton *et al.*, 2003).

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Appendix List of all species detected and number of census-plots in which the species were recorded in 1978, 1992 and 2003

Species	1978	1992	2003	Species	1978	1992	2003
Milvus migrans			4	*Monticola solitarius*	13	2	
Circaetus gallicus	2	3	1	*Turdus merula*	178	160	154
Circus pygargus		2	1	*Turdus viscivorus*	1		
Accipiter nisus	3	1		*Hippolais polyglotta*	6	44	28
Buteo buteo		1	9	*Sylvia undata*	76	23	18
Hieraaetus fasciatus	1			*Sylvia cantillans*	115	86	112
Falco tinnunculus	2	8	3	*Sylvia melanocephala*	76	96	76
Alectoris rufa	56	64	47	*Sylvia hortensis*	67	57	49
Phasianus colchicus	2	5		*Sylvia atricapilla*	85	119	130
Tetrax tetrax		1		*Phylloscopus bonelli*	27	15	17
Columbia livia			2	*Phylloscopus collybita*	9	5	13
Columba oenas	10			*Regulus ignicapillus*	9	64	99
Columba palumbus		23	42	*Aegithalos caudatus*	27	36	13
Streptopelia decaocto			6	*Parus cristatus*		6	3
Streptopelia turtur	86	74	81	*Parus ater*	1		
Clamator glandarius			1	*Parus caeruleus*	15	27	32
Cuculus canorus	69	44	66	*Parus major*	67	104	108
Otus scops	14		4	*Certhia brachydactyla*	4	11	41
Bubo bubo	6			*Oriolus oriolus*	18	14	14
Strix aluco	2		1	*Lanius excubitor*	1		
Apus apus	41	31	29	*Lanius senator*	17	13	3
Apus melba	4			*Garrulus glandarius*	30	43	21
Merops apiaster	1	4	2	*Pica pica*	18	27	15
Upupa epops	9	5	10	*Corvus monedula*	74	18	24
Picus viridis	12	14	3	*Corvus corone*	3	2	5
Galerida cristata	1			*Corvus corax*	15	9	9
Lullula arborea	24	17	51	*Passer domesticus*	8	4	4
Alauda arvensis	1			*Passer montanus*	2	1	
Ptyonoprogne rupestris	2			*Petronia petronia*	2		
Hirundo rustica	11	7	2	*Fringilla coelebs*	146	172	194
Delichon urbica	2			*Serinus serinus*	49	21	26
Anthus campestris		2	3	*Carduelis chloris*	50	4	8
Motacilla alba	1			*Carduelis carduelis*	20	8	28
Troglodytes troglodytes	2			*Carduelis cannabina*	6		
Erithacus rubecula	79	78	98	*Emberiza cirlus*	36	45	33
Luscinia megarhynchos	171	163	155	*Emberiza hortulana*	20	10	
Phoenicurus ochruros	8	3	5	*Emberiza calandra*	23	13	16
Saxicola torquata	7		1				