

Multi-scale study of bird species distribution and of their response to vegetation change: a Mediterranean example

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Abstract Land use changes operate at different scales. They trigger a cascade of effects that simultaneously modify the composition or structure of the landscape and of the local vegetation. Mobil animals, and birds in particular, can respond quickly to such multi-scalar changes. We took advantage of a long term study on the response of songbirds to land-use changes on four Mediterranean islands in Corsica and Sardinia to explore the benefits of a multi-scale analysis of the relationships between songbird distribution, vegetation structure and landscape dynamics. Field data and aerial photographs were used to describe the vegetation at three different scales. Birds were censused by point counts. We used statistical variance decomposition to study how bird distribution and vegetation at various scales were linked. We analysed multi-scale vegetation changes (floristic composition, plot vegetation type, and landscape structure) and their consequences on bird distribution with multivariate and non-parametrical tests. The distribution of most species was linked to at least two spatial scales. The weight of a given scale was consistent with life-

history traits for species whose biology was well-known. In the examples studied, vegetation composition, vegetation type and landscape changes that resulted from land abandonment negatively affected birds depending on open or heterogeneous areas. Our results emphasize that multi-scale analyses can greatly enhance our understanding of bird distribution and of their changes. Management of these populations should take into account measures at various spatial scales depending on the sensitivity of the species.

Keywords Scale · Land-use change · Landscape · Terrestrial bird community · Variance decomposition · Vegetation composition and structure · Island

Introduction

Scale can be defined as the spatial, temporal and organisational dimensions at which patterns and processes are observed and characterised (Marceau 1999). Ecological patterns depend on processes acting at different scales. For instance, at a regional scale, climate and history mainly explain species distribution, but at a local scale, biotic interactions are the main process regulating distributions (Levin 1992). Ecological processes are also simultaneously influenced by factors acting across a wide range of scales. The choice of scales in ecological studies will thus necessarily

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influence the results that can be demonstrated. This choice should therefore depend on the species studied and on the questions raised (Wiens 1989).

Landscape ecologists have developed concepts and methods around scale and scaling, such as patch dynamics theory, landscape resistance and connectivity, mosaic and heterogeneous landscape dynamics (Forman and Godron 1986; Wiens et al. 1993; Burel and Baudry 1999). Wu and Loucks (1995) proposed an integrated framework, the hierarchical patch dynamics paradigm. It considers the patch as the central unit and links hierarchy and patch dynamics theories. It focuses both on the vertical structure of the landscape, viewed as a number of discrete hierarchical levels, and on the spatial heterogeneity and interactions among the horizontal components. Patterns and processes at a focal spatial scale (e.g. a habitat patch) can be constrained by phenomena at a broader scale (e.g. the landscape), and explained by phenomena acting at a narrower scale (e.g. plant composition).

Since a few years, multi-scale approaches have been developed to study ecological systems (Cushman and McGarigal 2002; Grand and Cushman 2003) and to explore the importance of a range of scales in the distribution of animals and in the structure of their communities (Herrando and Brotons 2002; Stephens et al. 2003). The objective was to understand which processes act at each scale, how adjacent scales interact, or how species vary in their sensitivity to a given scale. Terrestrial birds, for example, depend on vegetation composition, structure and dynamics for food, shelter and reproduction (e.g. Bersier and Meyer 1994; Fleishman et al. 2003). Their sensitivity to the local vegetation or to landscape structure, will depend on their life history traits and on their habitat selection (Jökimäki and Huhta 1996; Tworek 2002; Skowno and Bond 2003, Brotons et al. 2005). A species' sensitivity to changes at the landscape scale will depend on its degree of habitat specialisation (Howell et al. 2000): generalists should be less affected than specialists or than species that require multiple habitat types to complete their cycle.

We investigated the potentials of a multi-scale approach in a study on the consequences of land-

use changes on the distribution of terrestrial birds within a Mediterranean landscape. In the European Mediterranean context, grazing abandonment and high tourist pressure modify patterns of land use. In this region, humans have interacted with their natural environment for thousands of years which resulted in particular landscapes (Lepart and Debussche 1992). Grazing was the main activity and maintained open pastures within a mosaic of matorrals and forests (Blondel and Aronson 1999). Land use changes have affected locally the composition and structure of plant and animal communities, and generated regional changes in landscape composition and physiognomy (Debussche et al. 1996; Preiss et al. 1997; Romero-Calcerrada and Perry 2004). Terrestrial birds, which range daily within tens or hundreds metres around their nest sites (Cramp 1977), are likely to be sensitive to such land-use changes (Suarez-Seoane et al. 2002; Sirami 2003).

We addressed three questions: 1—Which spatial scales best explain the composition of the terrestrial bird community and the distribution of each species? 2—At which spatial scales do environmental changes consecutive to land abandonment occur and at which scales should they be measured? 3—How do vegetation changes affect bird communities?

Materials and methods

Geography and history of the study area

Islands, delimited by the sea, are often considered as 'models' to gain insights on ecological dynamics (Vitousek 2002). Archipelagos can offer ecologically similar islands that differ in their history of human occupation. We studied four islands situated between Corsica (Cavallo, 112 ha, 32 m asl, granitic substrate) and Sardinia (Razzoli, 154 ha, 65 m asl, granitic substrate; Santa Maria, 205 ha, 49 m asl, schist substrate; Spargi, 420 ha, 155 m asl, granitic substrate; Fig. 1; 9° 19'E, 41° 17'N). Relatively similar in size, altitude, geology, climate and vegetation, their landscape was a fine-grained mosaic of matorrals (shrublands dominated by evergreen shrubs). Low-canopy-height matorrals were characterised by

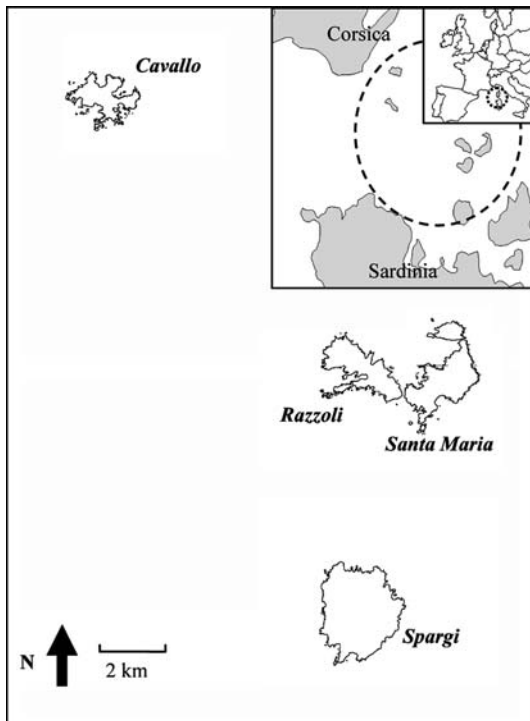


Fig. 1 Geographic location of the study area

Cistus monspeliensis L. and *Genista corsica* Lois. Medium-canopy-height matorrals were dominated by *Pistacia lentiscus* L. and *Juniperus phoenicea* L., high-canopy matorrals by *Arbutus unedo* L. and *Erica arborea* L. Dry herbaceous grasslands shaped by grazing were dominated by *Brachipodium phoenicoides* L., *Asphodelus microcarpus* Salzm. or *Helichrysum bracteatum* Vent. Except a few plantations of Pine (*Pinus* sp.) or Olive-tree (*Olea europaea* L.), trees were rare.

Agriculture has occurred on the four islands for at least two millenarries but has declined since the end of the 19th century. This decline accelerated between the two World Wars (Racheli 1982). Cattle breeding, the main activity, has been abandoned on all islands shortly before or just after the onset of this study. On Santa Maria, a sheep herd was still grazing. On Cavallo, urbanisation linked to tourism led to the construction of houses in large lots linked by dirt roads. Introduced wild boars occurred on Spargi and pheasants on Santa Maria. The visible impact of boars on the landscape dramatically increased during the study. Their ecological impact could be significant. The differ-

ences among islands in the amount of buildings present, in recent human use, or in the initial proportion of different habitat types account for small but noticeable differences in the composition and structure of their bird communities (see Appendix Table 5 and Thibault et al. 1990 for specificity of avifauna of each island).

In 1987, 167 census points were distributed over the entire area of the islands. Each plot was visited by one of three observers (I. Guyot, J.-L. Martin, and J.-C. Thibault). Each observer visited a comparable proportion of census points on each island. The points visited by each observer were distributed, whenever possible, over the entire area of an island to minimise observer related spatial biases. The position of the points was recorded on a 1/25,000 map. In 2003, the same points were sampled by the same observers. Their position was recorded with a GPS (Global Positioning System). Twenty five of the original points could not be relocated with accuracy or had become inaccessible (private property, built up area) leaving a total of 142 repeated census points (20 on Cavallo, 31 on Razzoli, 49 on Santa Maria and 42 on Spargi). Although each observer ensured that adjacent points did not overlap (i.e. had little chance to contact the same birds), when points from all observers were mapped mean distance between adjacent points was only of about 140 m, and 26 points out of a total of 142 census plots ended up to be at less than 100 m from their closest neighbours.

Sampling of bird data

We sampled birds by point-counts (Blondel et al. 1981; Bibby et al. 1992), and recorded terrestrial birds seen or heard during 10 min at each census point without limiting distance (20–31 May 1987 and 21–30 May 2003). In such censuses, birds recorded typically occur at less than 100 m from the observer and most are observed within 50 m. Birds were counted during the first hours after sunrise and in the absence of rain or strong wind. Nocturnal and aerial birds were excluded (Bibby et al. 1992). We split each count in two 5-min periods to estimate observer related bias on species detectability with capture–recapture

methods (MacKenzie et al. 2002). There was no detectable observer related bias.

Because a few point counts were relatively close to each other, some limited level of spatial autocorrelation could occur. However, calculation of Moran I index (Moran, 1950) through the RookCase software (Sawada 1999), indicated a lack of spatial autocorrelation in species richness on each of the four islands.

Vegetation data

Flora variables and songbird foraging scale

We described the vegetation structure at the scale of a songbird's foraging behaviour by measuring, within a virtual circle of 25 m in radius around the sampling point, the percent cover of the main plant species, their maximum height, the maximum height of the vegetation, the height at which canopy closure reached 25%, 50%, and 75% respectively (open canopy, medium canopy, dense canopy), and the cover of rock or bare soil. We used a Principal Component Analysis (PCA) to eliminate redundant or highly correlated variables and retained six 'flora variables' for the analyses (Table 1): the maximum height of the vegetation (*Hmax*), the percent cover of *Erica arborea* (*Earb*), *Juniperus phoenicea* (*Jpho*), *Genista corsica* and *Calicotome spinosa* (*Geca*),

Cistus monspeliensis (*Cmon*), and of rock or bare soil (*Rock*).

Plot composition variables and territory scale

To describe the vegetation around census points at a broader scale that matches the scale of a songbird territory, we used 1989 black and white photographs of Razzoli, Santa Maria and Spargi and real colour photographs from 1998 for Spargi and from 1999 for Razzoli and Santa Maria (Compagnia Generale Ripresearee). For Cavallo, we used infrared pictures from 1985 and 2000 (Inventaire Forestier National). These photographs were those that best matched the years when field data were collected. We used a PCA on the three bands (red, blue and green) of the true colour pictures to transform them into black and white photographs. We used the first component extracted from the PCA as the black and white transformed photograph. This first component explained at least 99.5% of the initial variance in each photograph. The photographs could then be classified with the same method. Photographs were ortho-rectified and geo-referenced with ENVI 3.6 (Research System Inc., Boulder, Colorado).

Supervised classification methods with ENVI 4.0 (parallelepiped method for black and white photographs, maximum likelihood method for

Table 1 Description of vegetation variables

Variable set	Variable name	Description
Flora (25 m)	<i>Hmax</i>	Maximum vegetation height (m)
	<i>Earb</i>	Percent cover of <i>Erica arborea</i> (%)
	<i>Jpho</i>	Percent cover of <i>Juniperus phoenicea</i> (%)
	<i>Geca</i>	Percent cover of <i>Genista corsica</i> and <i>Calicotome spinosa</i> (%)
	<i>Cmon</i>	Percent cover of <i>Cistus monspeliensis</i> (%)
	<i>Rock</i>	Percent cover of <i>Rock or bare soil</i> (%)
Plot composition (50 m)	<i>Pmhigh</i>	Proportion of pixels classified as high matorral (%)
	<i>Pmmed</i>	Proportion of pixels classified as medium matorral (%)
	<i>Pmlow</i>	Proportion of pixels classified as low matorral (%)
	<i>Pgrass</i>	Proportion of pixels classified as grassland (%)
	<i>Prock</i>	Proportion of pixels classified as rock or bare soil (%)
	Landscape (200 m)	<i>Nbmat</i>
<i>Nbgrass</i>		Number of 'mainly grassland' patches
<i>Nbrock</i>		Number of 'mainly rock or bare soil' patches
<i>Smat</i>		Mean area of 'mainly high matorral' patches (m ²)
<i>Sgrass</i>		Mean area of 'mainly grassland' patches (m ²)
<i>Srock</i>		Mean area of 'mainly rock or bare soil' patches (m ²)
<i>Ssea</i>		Area of Sea (m ²)

infrared photographs) were used to define five vegetation classes: rock or bare soil (class 1), grassland (class 2), low matorral (class 3, corresponding to canopy height lower than approximately 50 cm), medium matorral (class 4, corresponding to canopy height between approximately 50 cm and 2 m), and high matorral (class 5, corresponding to canopy height higher than approximately 2 m). In these classifications, a pixel corresponded to a one-metre square on the ground. We used confusion matrixes to estimate the quality of classifications. More than 84.5% of the pixels of the test zones were classified in the right class for all islands (Table 2). We calculated the percentage of pixels classified in each of the 5 classes, within a radius of 50 m around each census point, an area slightly smaller than one hectare. We defined five ‘plot composition’ variables (Table 1): *Prock* (percent cover of rock and bare soil), *Pgrass* (percent cover of grassland), *Pmlow* (percent cover of low matorral), *Pmmed* (percent cover of medium matorral) and *Pmhigh* (percent cover of high matorral).

Landscape variables and habitat diversity scale

We exported vegetation classifications in ArcGIS 8.3 (Environmental Systems Research Institute, Inc.). After photo-interpretation of the classifications, we assigned each patch of homogeneous

vegetation to four vegetation types based on the vegetation class that dominated the patch: ‘mainly rock or bare soil’; ‘mainly grassland’; ‘mainly matorral’; ‘mainly high matorral’. We individualised patches of matorral vegetation when one of their dimensions exceeded 100 m. We individualized patches of grassland and rock or bare soil when one of their dimensions exceeded 20 m because of our focal interest for grazing abandonment. We estimated that a 200 m radius was representative of the diversity of habitats available to a terrestrial bird. Within this 200 m radius, we calculated for each census point the number of patches of each vegetation type, their mean area (except for the ‘mainly matorral’ type which we considered the landscape matrix) and the mean area covered by sea. This defined seven variables describing the ‘landscape’ (Table 1). The dense coverage of the islands by census points entails spatial overlap of the areas captured by a 200 m radius around adjacent census points. Thus, while flora and plot composition measures for adjacent census points can be considered as independent, this is not so for landscape measures: individual birds from adjacent census point share a portion of the same landscape.

Hereafter, first year will refer to 1987 for census points, to 1985 for the aerial photograph of Cavallo and to 1989 for the photographs of Razzoli, Santa Maria and Spargi. Second year will refer to 2003 for census points, to 2000 for the photograph of Cavallo, to 1999 for the photographs of Razzoli and Santa Maria and to 1998 for the one of Spargi.

Table 2 Quality of vegetation classifications, quantified with confusion matrix

Island	Year	Global precision ^a	Kappa ^b
Cavallo	1985	88.10	0.84
	2000	97.52	0.96
Razzoli	1989	88.13	0.85
	1999	84.51	0.80
Santa Maria	1989	88.54	0.85
	1999	88.93	0.86
Spargi	1989	88.65	0.86
	1998	90.96	0.88

Year = year of photography

^a Mean percentage of correctly classified pixels in test zones

^b The Kappa coefficient measures how well the classification performed compared to the probability of randomly assigning points to their correct categories in the test zones

Data analyses

Our data set is a series of matrixes, where Y is the table of dependent variables (birds’ occurrence for each census point) and X tables of explanatory variables. We analysed the relationship between bird community structure (Y) and vegetation variables (the three sets of variables in Table 1) with Canonical Correspondence Analyses (CCA, Ter Braak 1987; Prodon and Lebreton 1994). Sixteen years separated bird censuses. We therefore considered that the relation between bird distribution and vegetation was independent between the two years and we pooled them in a single data set. We used a statistical partitioning

of the variance by a series of partial CCA (Cushman and McGarigal 2002) to split the explained species–environment relationship variance between the different sets of variables (flora, plot composition and landscape). To interpret the species responses to each set of vegetation variables, we used the biplots of the conditional flora model (plot composition and landscape as covariates), the conditional plot composition model (flora and landscape as covariates) and the conditional landscape model (flora and plot composition as covariates; see Grand and Cushman 2003). For each species (i.e. each column of the Y matrix) we studied the relationship between its distribution and the vegetation variables (Table 1) with a linear-logistic model (binomial distribution and link function logit, McCullagh and Nelder 1989). As we could not include 18 variables in this analyses, we used the first and the second components of a PCA for each set of variable (flora, plot composition and landscape), to summarise our dataset by 6 variables for this analysis (Table 3). In the same way as for the multivariate analyses, variance was decomposed between flora, plot composition and landscape effects through a series of linear-logistic models (Legendre and Legendre 1998).

Table 3 Summarised variables extracted from the PCA of each set of variable (F1: first principal component, F2: second principal component)

Variable set	Variable	F1	F2
Flora	<i>Hmax</i>	0.79	-0.21
	<i>Earb</i>	0.07	-0.62
	<i>Jpho</i>	0.57	0.55
	<i>Geca</i>	-0.37	-0.07
	<i>Cmon</i>	-0.35	-0.57
	<i>Rock</i>	-0.55	0.60
Plot composition	<i>Pmhigh</i>	-0.62	0.55
	<i>Pmmed</i>	-0.87	-0.33
	<i>Pmlow</i>	0.53	-0.74
	<i>Pgrass</i>	0.85	0.09
	<i>Prock</i>	0.56	0.66
	<i>Nbmat</i>	-0.25	-0.61
Landscape	<i>Nbgrass</i>	-0.63	-0.03
	<i>Nbrock</i>	-0.68	-0.14
	<i>Smat</i>	0.76	0.03
	<i>Sgrass</i>	-0.04	0.16
	<i>Srock</i>	-0.28	0.64
	<i>Ssea</i>	-0.14	0.77

For acronym definitions see Table 1

We studied changes in vegetation over the whole area. We randomly selected 50 points in each vegetation type defined in the first year of the study. These points were at least 20 m apart, and at least at 10 m from the patch edge. In one vegetation type, ‘mainly high matorral’ on Razzoli island, the area of the vegetation type available was limited and we selected only 20 points. We calculated the mean vegetation class of the pixels within a 10 m radius around these points, in the first and in the second year. We compared these means with a *t*-test for paired data: if the mean class value increased, the vegetation was higher the second year of study. We repeated this analysis five times for each island, and considered that the changes were significant if the five repetitions were significant. We also studied vegetation changes at the census points. We used a non-parametric test for paired data (Wilcoxon’s test of mean comparison) to study the changes of each variable (Table 1) between the two years, on each island.

We used a PCA to analyse bird community changes for each island (Y). Species contacted in less than five census points were excluded from the analyses. We preferred PCA over Canonical Analysis, because we wanted to take into account census points’ species richness (Legendre and Legendre 1998). For each island we produced two biplots. Bird census points were placed in the F1-F2 biplot. We linked the census point of 1987 to the corresponding census point in 2003 with an arrow to visualise changes in bird community for each census point. Because the distribution of the coordinates was not normal we tested the significance of the changes in the coordinates of a census point between the two years with a non-parametric test (Wilcoxon’s mean comparison for paired data).

The proximity between some census points can lead to overestimating some of the trends due to spatial autocorrelation. On the one hand, geographically contagious biotic processes (migration, population structure) can promote biologically meaningful spatial autocorrelation in species distribution (Griffith and Peres-Neto 2006). On the other hand, spatial autocorrelation is known to influence the interpretation of statistical models by affecting tests of significance of the

association between species distribution and environmental factors, as well as calculated correlations among such variables (Selmi et al. 2003; Legendre et al. 2002). Spatial autocorrelation can be handled by using specific statistical methods (see Augustin et al. 1996; Legendre et al. 2002; Lichstein et al. 2002). The protocol defined in 1987 and repeated in 2003 does not allow the full use of the statistical methods including spatial autocorrelation, especially because of a lack of sufficient sample size for a given island. However, the residuals of linear models did not show spatial autocorrelation at short distances, when island specificity was controlled for, except for *Sylvia sarda*, *Troglodytes troglodytes*, *Phasianus colchicus* and *Carduelis chloris* and to a lower extent *Sylvia undata* and *Parus major* (Moran correlograms, RookCase software). In the multivariate analyses where we pooled the data from all islands, spatial autocorrelation of bird distribution linked to island specificity may explain part of the variance attributed to the variables studied, but we do not think that this affects the proportion of the variance explained by each set of variables and hence the validity of our conclusions.

We used the softwares STATISTICA 6.1 (StatSoft 1984) and SAS v.8 (Sas Institute 1999) for statistical tests and linear models. STATISTICA, R 1.9.0. (R Development Core Team 2004) and CANOCO 4.5 were used for multivariate analyses. A probability of Type I error of 0.05 or less was accepted as significant.

Results

Which spatial scale best explained terrestrial bird distribution?

Vegetation variables explained 20.5% of the variance in bird community structure. Each set of variable (flora, plot composition or landscape) accounted for almost a half of the variance explained by vegetation variables (Fig. 2a). The interactions between flora and plot composition variables and between plot composition and landscape variables were high (respectively 8.2% and 12.7% of the variance explained by vegetation variables).

F1-F2 biplots of the conditional models described the portion of community structure that is explained by a given set of variables (flora, plot composition or landscape). The first axis of the flora conditional model summarised 48.2% of the variance of the species data explained by the flora variables (Fig. 2, b1). This axis segregated species associated to mosaics of patches of vegetation dominated by *Erica arborea* and patches of rocks or bare soil (negative scores) from species associated to mosaics of vegetation dominated by *Juniperus phoenicea* and of vegetation dominated by *Genista corsica* or *Calicotoma spinosa* (positive scores). In the *Erica arborea* rock mosaics, species like *Erithacus rubecula* were associated to the vegetation patches dominated by *Erica arborea*. *Monticola solitarius* was associated to the patches dominated by rocks and bare soil. In the *Juniperus/Genista* mosaics the two species with the highest scores on axis 1 were *Phasianus colchicus* and *Emberiza cirrus*. The second axis of the flora conditional model summarised 24.9% of the variance of the species data explained by the flora variables. It segregated species such as *Anthus campestris*, *Saxicola torquata* and *Sylvia sarda*, all observed in the lowest matorral patches dominated either by *Cistus monspeliensis* or by *Genista corsica* (negative scores), from species such as *Regulus ignicapillus* and *Sylvia cantillans* observed in the tallest vegetation.

The first axis of the plot composition model summarised 34.0% of the variance of the species data explained by plot composition variables (Fig. 2, b2). It segregated census plots with a significant cover of rocks and bare soil or of grassy vegetation (positive scores) from all other plots (negative scores). *Passer domesticus* was the species strongly associated to this axis. The second axis of this model summarised 26.0% of the variance of the species data explained by plot composition variables. This axis segregated plots dominated by low matorrals (positive scores) and their associated species from plots dominated by medium matorrals (negative scores). *Monticola solitarius* was the species most associated with low matorrals and *Parus major*, *Regulus ignicapillus* and *Sylvia cantillans* were those most associated with medium matorrals.

Overall species segregation was less marked than for the two other scales of analysis.

The first axis of the landscape model summarised 34.7% of the variance of the species data explained by landscape variables (Fig. 2, b3). It segregated plots in landscape mosaics characterised by a large number of grassy and matorral patches, with large areas of rock and bare soil

situated close to the shores from plots in landscapes with large grassy patches. *Phasianus colchicus* was associated with the latter, *Passer domesticus* with plots from coastal areas with a large number of shrubby patches and *Sylvia cantillans* with parts of the mosaic that had fewer (and thus larger) matorral patches interspersed with numerous (but small) grassy patches. The

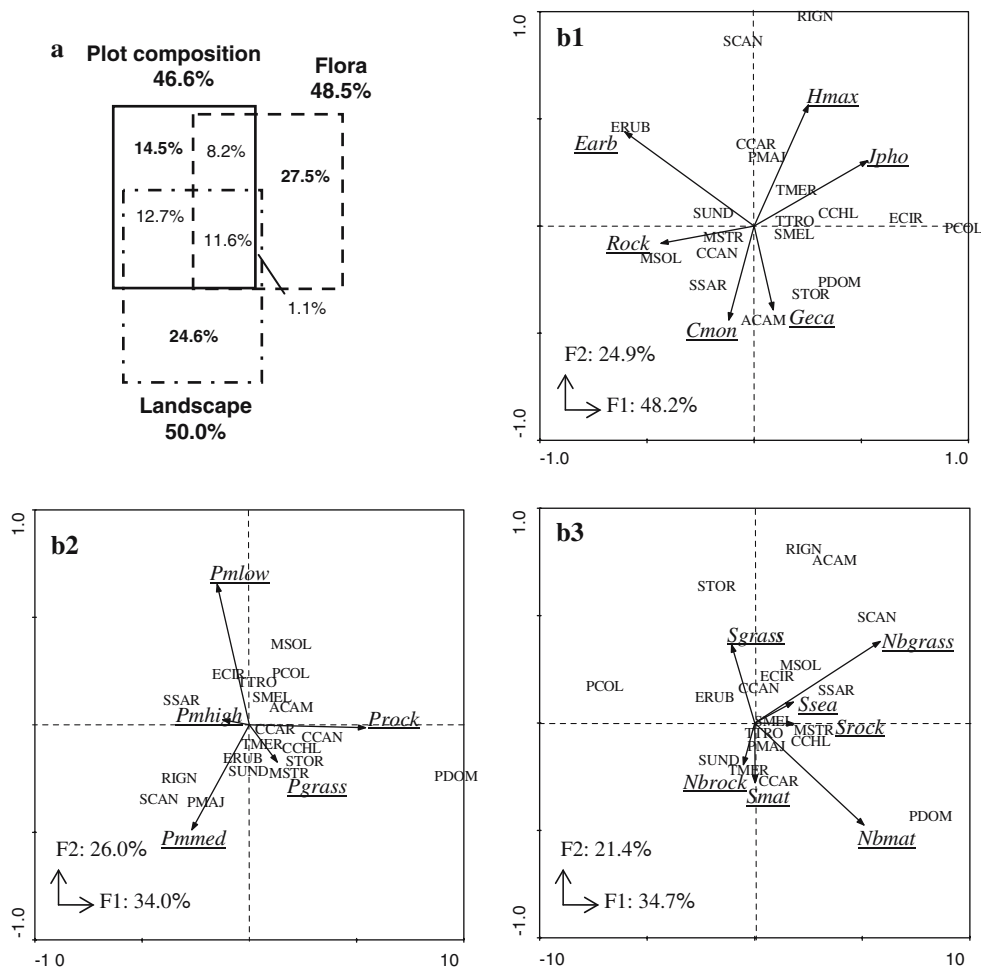


Fig. 2 Decomposition of the variance between the three sets of vegetation variables. **(a)** Variance partitioning Venn diagram representing percentage of unique and shared contribution of flora (*dashed line*), plot composition (*continuous line*) and landscape (*dotted and dashed line*) variables to the variance explained by vegetation variables. The area of each square is proportional to the percent of explained variance. The intersection between the squares represents the percent of explained variance due to the interaction of two or three sets of variables. **(b)** Canonical

Correspondence Analysis: **b1**: Flora conditional model (Plot composition and landscape as covariates), **b2**: Plot composition conditional model (Flora and landscape as covariates), **b3**: Landscape conditional model (Flora and plot composition as covariates). Species data-points are at the bottom left corner of their name. Vegetation variables are underlined. The weight of the axis is the percent of variance explained by the axis within the conditional model. For variable and species acronyms, see Table 1 and Appendix Table 5

second axis of the landscape model summarised 21.4% of the variance of the species data explained by landscape variables. It segregated plots from landscapes dominated by high matorrals with numerous small rocky patches (negative

scores) and plots from landscapes with large grassy patches or numerous small grassy patches. *Carduelis carduelis*, *Turdus merula* and *Sylvia undata* were associated with big patches of high matorrals and with small patches of rock or bare

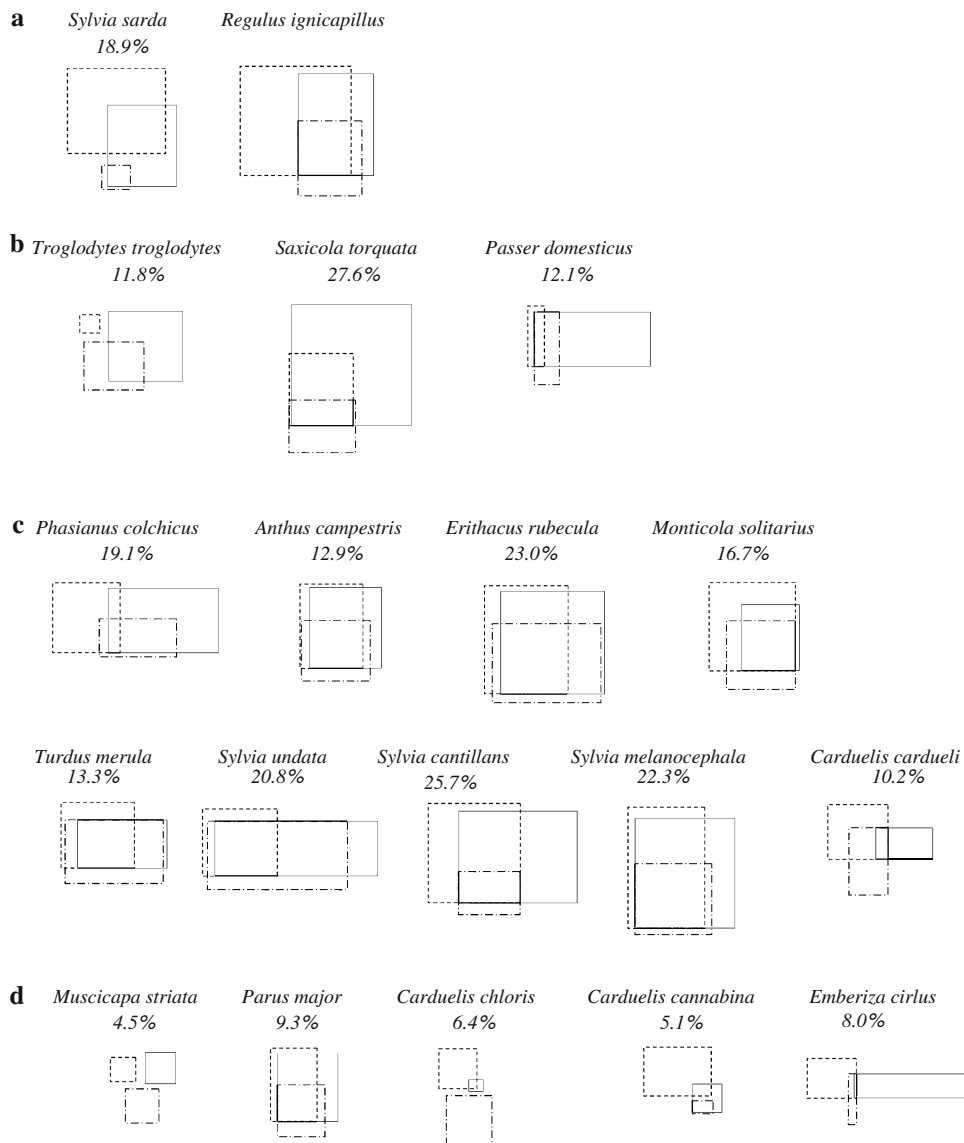


Fig. 3 Variance partitioning Venn diagrams representing percentage of unique and shared contribution of flora (dashed line), plot composition (continuous line) and landscape (dotted and dashed line) variables. Species whose distribution is mainly explained by: (a) Flora variables, (b) Plot composition variables, (c) Two or three sets of

variables, (d) No variables (less than 10% of variance explained by vegetation variables). The area of each square is proportional to the percent of variance explained. The intersection between the squares represents the percent of variance explained by the interaction of two or three sets of variables

soil (positive scores). *Passer domesticus* was associated with numerous patches of high matorrals, *Saxicola torquata* with big patches of grassland, *Sylvia cantillans* with small and numerous patches of grassland (negative scores). Of all three scales, the flora scale shows the strongest segregation among species. At both the plot and landscape scales however a significant proportion of the species were poorly segregated by the variables under study.

Linear-logistic models explained from 4.52% to 27.60% of the variance of the distribution of the birds, depending on the species (Fig. 3). The percent of variance explained by a given set of variable, i.e. the area of the three rectangles on the figure, varied a lot between species. In two species, *Sylvia sarda* and *Regulus ignicapillus*, flora variables did summarise more than 40% of the variance explained by the vegetation. In three species, plot composition variables summarised more than 40% of the variance explained by the vegetation: *Troglodytes troglodytes*, *Saxicola torquata* and *Passer domesticus*. In no species did landscape variables summarize more than 40% of the variance explained by the vegetation. The distribution of nine species was explained by two or three sets of variables. The distribution of five species was not explained by the variables selected at the three different scales (less than 10% of the variance): *Muscicapa striata*, *Carduelis cannabina*, *Carduelis chloris*, *Emberiza cirulus* and *Parus major*. The interaction between the sets of variables, i.e. the intersection between the rectangles, varied from species to species. The interaction was for instance small for *Passer domesticus* and large for *Sylvia melanocephala*.

At which scale did vegetation change?

Within each vegetation type, defined in the first year of study, vegetation changes depended on the island (Fig. 4). On Cavallo, vegetation height of ‘mainly grassland’ and ‘mainly high matorral’ vegetation types decreased between the two years. On Razzoli, Santa Maria and Spargi, vegetation height increased in types ‘mainly grassland’ and ‘mainly rock or bare soil’. Vegetation height also increased in vegetation type ‘mainly matorral’ on Santa Maria. On Spargi

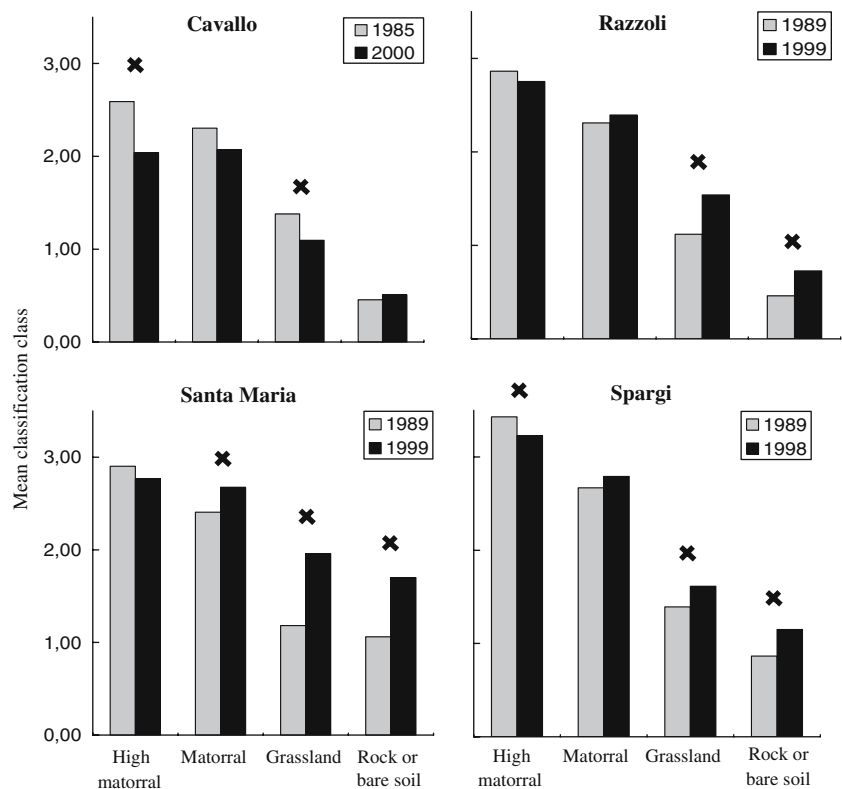
vegetation height decreased in the ‘mainly high matorral’ vegetation type. In sum, vegetation became denser on Razzoli, Santa Maria and Spargi; grasslands were replaced by bare soil on Cavallo.

Only a few flora variables changed significantly between 1987 and 2003 (Table 4). On Cavallo, the maximal height of the vegetation and the percent cover of high matorral increased (*Hmax* $Z_{(1)} = 2.154$ $P = 0.031$, *Pmhigh* $Z_{(1)} = 2.389$ $P = 0.017$). The percent cover of rock or bare soil and the area of rock and bare soil patches increased (*Prock* $Z_{(1)} = 3.360$ $P < 0.001$, *Srock* $Z_{(1)} = 3.024$ $P = 0.002$). Moreover, the percent cover of grassland, the number of grassland patches and their area decreased between the two years of study (*Pgrass* $Z_{(1)} = 3.509$ $P < 0.001$, *Nbgrass* $Z_{(1)} = 2.670$ $P = 0.008$, *Sgrass* $Z_{(1)} = 3.808$ $P < 0.001$). On the three Sardinian islands, the cover percent of medium matorral (*Pmmed*) increased whereas the cover percent of grassland (*Pgrass*) decreased (Table 4). The number and the area of grassland patches (*Nbgrass* and *Sgrass*) decreased, the number of rock or bare soil patches (*Nbrock*) increased whereas their area (*Srock*) decreased: they became fragmented. Some differences between the Sardinian islands can be observed: an increase in high matorral percent cover on Razzoli (*Pmhigh* $Z_{(1)} = 4.860$ $P < 0.001$), an increase in rock or bare soil at a local scale on Santa Maria (*Rock* $Z_{(1)} = 2.660$ $P = 0.008$), and an increase in rock or bare soil percent cover on Spargi (*Prock* $Z_{(1)} = 3.168$ $P = 0.002$).

What were the consequences of these changes for the terrestrial birds?

In 1987, we recorded 19 species, 17 in 2003. Multivariate analyses showed that, overall, on Cavallo, census point coordinates shifted along axis 2, toward negative values ($Z_{(1)} = 2.090$ $P = 0.037$, Fig. 5a). *Passer domesticus* and *Anthus campestris* were associated with positive values of the axis 2 coordinates. Their frequency of observation decreased between the first and the second year, whereas *Carduelis chloris* and *Monticola solitarius* were associated with negative values and had higher observation frequencies in the

Fig. 4 Changes in mean vegetation class, for each vegetation type (defined in the first year), on each island. When each repetition (see methods) is significant, vegetation types are noted with a cross. A significant test indicates that the vegetation of the vegetation types' changes: if the class value increases, the vegetation is on average higher in the second year; if the class value decreases, the vegetation is on average lower



second year. On Razzoli, census point coordinates shifted along axis 2 toward negative values ($Z_{(1)} = 3.347$ $P < 0.001$, Fig. 5b). *Monticola solitarius*, *Carduelis carduelis*, *Saxicola torquata* and *Anthus campestris* disappeared from some census points whereas *Sylvia melanocephala* and *S. undata* appeared. On Santa Maria, census point coordinates shifted along axis 2 toward positive values ($Z_{(1)} = 4.564$ $P < 0.001$, Fig. 5c). This was associated to an increase in occurrence of *Phasianus colchicus* and *Sylvia undata* and to a decrease in occurrence of *Turdus merula*. On Spargi, census point coordinates shifted significantly along both axis (axis 1: $Z_{(1)} = 3.657$ $P < 0.001$, axis 2: $Z_{(1)} = 4.470$ $P < 0.001$, Fig. 5d). Along the first axis, *Sylvia sarda* disappeared from some census points whereas *Erithacus rubecula*, *Turdus merula*, *Parus major* and *Muscicapa striata* appeared. Along the second axis, census points initially characterised by *Troglodytes troglodytes*, *Sylvia cantillans* and *Parus major* became characterised by *Sylvia undata*, *Turdus merula* and *Carduelis cannabina*.

Discussion

Which spatial scale best explained terrestrial bird distribution?

In keeping with other studies (Herrando and Brotons 2002; MacFaden and Capen 2002; Cushman and McGarigal 2002; Moreira et al. 2005), bird community structure and species distribution were explained by interactions of sets of vegetation variables from different spatial scales.

Each set explained an equal proportion of the relationship between the bird community and the vegetation. Using them together improved the description of the link between community structure and vegetation. Plot composition variables as such (not in interaction with the other variables) explained only about 14.5% of the data variance. The variables at this intermediate scale had strong interactions with variables from both the flora and landscape scales. This suggests that the variations described at this scale are partly redundant with other scales. Matorral types (plot

Table 4 Changes in vegetation variables between the first and the second year for each island

Variable set	Variable	Cavallo			Razzoli			Santa Maria			Spargi						
		First year ^a	Second year	Z ^b	P-value ^c	First year	Second year	Z	P-value	First year	Second year	Z	P-value				
Flora	<i>Hmax^d</i> (m)	2.4	3.0	2.154	0.031 ^{ab}	1.5	1.4	0.360	0.719	3.1	3.0	0.652	0.514	3.0	3.0	0.704	0.481
	<i>Earb</i> (%)	3.6	1.4	1.260	0.208	5.3	5.3	0.312	0.755	0.0	0.0			14.0	14.7	0.615	0.538
	<i>Jpho</i> (%)	16.4	10.0	1.742	0.082	10.1	11.6	1.0266	0.305	25.6	25.3	0.381	0.703	13.2	10.7	0.625	0.532
	<i>Geca</i> (%)	1.9	0.7	1.753	0.080	6.4	5.5	0.698	0.485	5.0	3.6	0.780	0.435	0.7	1.4	1.333	0.182
	<i>Cnon</i> (%)	21.1	16.5	0.970	0.332	29.6	23.0	2.298	0.022 [*]	23.0	18.1	1.832	0.067	27.6	23.3	1.573	0.116
	<i>Rock</i> (%)	6.7	12.9	1.278	0.201	19.8	18.0	0.660	0.509	6.0	9.4	2.660	0.008 ^{**}	5.9	8.1	1.235	0.217
	<i>Pnhigh</i> (%)	8.0	13.1	2.389	0.017 [*]	0.9	4.8	4.860	<0.001 ^{***}	7.1	5.4	1.666	0.096	14.6	16.7	1.919	0.055
	<i>Pnmed</i> (%)	22.5	21.4	0.635	0.526	24.4	32.3	2.273	0.023 [*]	38.9	49.6	3.894	<0.001 ^{***}	49.1	50.9	1.032	0.302
	<i>Pnlow</i> (%)	23.1	17.9	1.978	0.048 [*]	39.1	38.8	0.118	0.906	29.4	28.8	0.462	0.644	21.6	20.0	1.207	0.228
	<i>Pgrass</i> (%)	19.6	10.9	3.509	<0.001 ^{***}	26.6	15.2	3.782	<0.001 ^{***}	17.9	9.4	4.073	<0.001 ^{***}	13.4	8.7	2.970	0.003 ^{**}
Landscape	<i>Prock</i> (%)	20.8	33.7	3.360	<0.001 ^{***}	8.0	8.1	0.059	0.953	5.5	5.2	0.015	0.988	1.3	3.5	3.168	0.002 ^{**}
	<i>Nbnut</i>	4.9	5.4	0.075	0.940	2.4	7.1	4.660	<0.001 ^{***}	6.1	2.7	3.431	<0.001 ^{***}	4.1	3.7	1.163	0.245
	<i>Nbgrass</i>	23.6	16.4	2.670	0.008 ^{**}	22.7	14.5	3.126	0.002 ^{**}	9.3	9.2	1.055	0.291	15.6	8.5	5.277	<0.001 ^{***}
	<i>Nbrock</i>	10.7	8.8	1.449	0.147	9.4	17.0	4.617	<0.001 ^{***}	9.6	10.8	2.241	0.025 [*]	2.8	6.9	5.212	<0.001 ^{***}
	<i>Snut</i> (m ²)	1,154	1,254	0.821	0.411	630	1,192	2.931	0.003 ^{**}	12,239	1,843	2.523	0.012 [*]	7,445	7,557	1.207	0.228
	<i>Sgrass</i> (m ²)	654	193	3.808	<0.001 ^{***}	1,618	508	4.311	<0.001 ^{***}	1597	404	5.207	<0.001 ^{***}	1,120	706	4.070	<0.001 ^{***}
	<i>Srock</i> (m ²)	3,426	7570	3.024	0.002 ^{**}	1,378	826	3.664	<0.001 ^{***}	960	614	4.585	<0.001 ^{***}	752	734	1.391	0.165

^a Mean value of the variable in the first year (next column: in the second year)

^b Wilcoxon's test for paired data

^c *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$

^d For the abbreviations, see Table 2

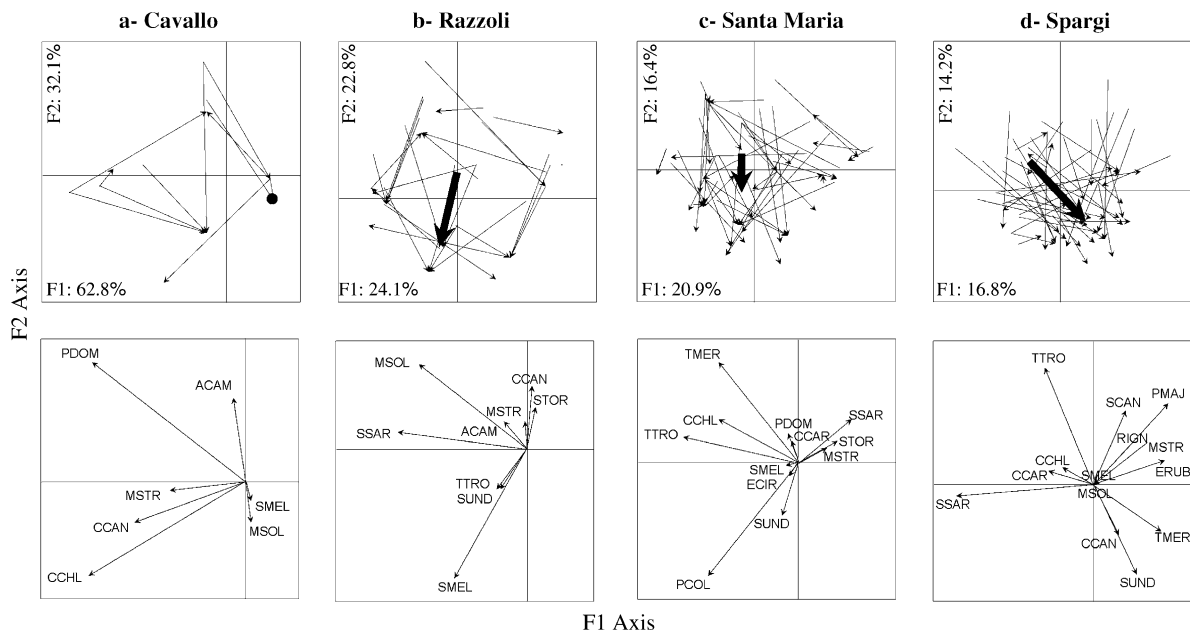


Fig. 5 F1-F2 bi-plots of non-normalized PCA of avifauna data. Census points coordinates changes between 1987 and 2003 are represented by thin arrows (*first row*). The wide arrow represents the changes in the median coordinates. On Cavallo, this shift cannot be illustrated by an arrow,

because *Sylvia melanocephala* is the only species recorded for more than half of the points, both in 1987 and in 2003. Species position is illustrated in the second row. Species abbreviations are in Appendix Table 5

composition scale) can indeed be described by their dominant plants (flora scale). Moreover, the area and number of matorral patches (landscape scale) are closely linked to plot composition.

Bird species differed in their response to the three spatial scales. However, for most species, at least two spatial scales had to be considered to properly account for species distribution. These scales can either have no interaction, as for *Phasianus colchicus*, or strong interaction, as for *Sylvia melanocephala*, *Erithacus rubecula* or *Anthus campestris*.

We can use the bird species/vegetation biplots (Fig. 3) to analyse the variance partitioning for each species (Fig. 4). The occurrence of *Phasianus colchicus*, for instance, was linked to both flora and plot composition variables with little interaction between scales (Fig. 4). At the flora scale this species was mainly associated to the percent cover of *Juniperus phoenicea*. At the plot composition scale, it was associated to the amount of low matorral (Fig. 3b). This is consistent with

the preference of this species for a mix of small clumps of *Juniperus* bushes for cover and for extensive low vegetation for foraging.

In the case of the *Sylvia* spp., the distribution of *Sylvia sarda* was best explained by the flora and plot composition variables. The flora variables as such seemed especially relevant as their intersection (interaction) with the other sets was limited (Fig. 4). In the flora conditional model (Fig. 3b), the presence of *Sylvia sarda* was correlated to the presence of *Cistus monspeliensis* and of rock or bare soil. This is consistent with the habitat selection described for this species by Martin and Thibault (1996). For *Sylvia undata*, a species morphologically close to *S. sarda*, plot composition variables (medium matorral on Fig. 3b) and landscape variables (number of rock or bare soil patches and area of matorral patches on Fig. 3b) best described distribution, with strong interactions between the two scales (Fig. 4). The presence of this species seems to depend on the amount of preferred habitat at the landscape

scale, to the contrary of *Sylvia sarda* which seems to be able to be present even if the right conditions occur only at the local scale. In other words, this species seems to be able to occur patchily, whereas *Sylvia undata* may need the presence of a small population. This has already been suggested based on direct observations by Thibault et al. (1990).

The distribution of *Sylvia cantillans* was best explained by flora and plot composition variables, with the plot composition variables predominant (Fig. 4). It was associated to vegetation maximum height and high cover of *Erica arborea* at the flora scale, and to high cover of medium matorral at the plot composition scale (Fig. 3b). The landscape scale interacted strongly with the two other scales and species occurrence was associated to the presence of numerous small grassland patches in the landscape. The response of this species to the three scales was consistent with its preference for heterogeneous matorrals that include small trees or large shrubs used to forage or to sing, and small open patches in a matrix of medium matorral to feed in (see Martin 1992; Martin and Thibault 1996). For *Sylvia melanocephala* each set of variables explained a large proportion of the variance of its distribution. There were strong interactions between the three scales (Fig. 4). The coordinates of this species were close to the origin in all three biplots (Fig. 3b). Its distribution could not be associated to particular vegetation variables. This can be explained by the fact that *Sylvia melanocephala* was the most widespread species and has been contacted in almost all census points.

Thus, despite spatial autocorrelation for some birds, we showed that the spatial scales which can explain the distribution of a bird species, and the interactions between scales, depend on the species' biology (especially habitat selection, according to foraging, shelter and reproduction needs).

At which scale did vegetation change?

The multi-scale comparison of the vegetation between the two years of our study has shown that vegetation changes occurred at all three

spatial scales: floristic composition, percent cover of vegetation types, and landscape structure. Grazing abandonment or decrease led to the colonisation of grasslands and bare areas by shrubby and woody vegetation, and to the fragmentation of open areas (Poyatos et al. 2003). In matorrals, vegetation height increased, but floristic composition did not change significantly. The landscape became more homogeneous. These changes are consistent with those described in previous studies on the consequences of grazing abandonment in the Mediterranean region (Le-part and Debussche 1992). On Cavallo, land abandonment led to the development of tourism and urbanisation. Areas of bare soil increased, with new dirt roads and houses. In some gardens, irrigation and plantations led to an increase in vegetation height.

Although these changes are perceptible at all three spatial scales they seemed less measurable at the local scale (3 tests out of 24 are significant for flora variables, compared to 17 out of 24 for landscape variables, Table 4). Field variables, such as plant cover estimates, had higher standard errors by nature and because of the approximate geographical localisation of the census points in 1987. Remote sensing methods seemed therefore more accurate to assess vegetation changes over the period. It is also possible that, in a heterogeneous landscape, where the number of plant species was limited, changes in vegetation height and structure were more prominent than changes in floristic composition. This may be accentuated in an island context where colonisation by new plant species is restricted.

What were the consequences of these changes for the terrestrial birds?

Most changes in bird species occurrences between the two years could be linked to changes in vegetation cover. Declining species were mostly species that depended on open areas or low matorrals (*Anthus campestris*, *Saxicola torquata*, *Sylvia sarda*) or on heterogeneous landscape (*Sylvia cantillans*). Species whose occurrence increased were species that depended on high

and close vegetation habitats as *Sylvia melanocephala*, *Erithacus rubecula* or *S. undata*.

The distribution of *Anthus campestris* was related to all three sets of variables in the analysis on species distributions. At each scale, the presence of this species was linked to variables associated to grasslands. The decline in number and area of grassland patches seems to be associated with the decline of this species. Similarly, the distribution of *Saxicola torquata* was mainly related to plot composition variables, and, in particular, to percent cover of grassland. The decrease in grassland cover at an intermediate scale on the islands where this species was contacted seems to be the mechanism involved in the decline of this species. This local decline contrasts with the stability of the species in reference areas on Corsica during the same period (Entraygue 2004). *Sylvia cantillans* was associated both to the number of grassland patches in the landscape, and to the maximal vegetation height at the local scale. This species depends on heterogeneous habitat structure (Martin 1992; Martin and Thibault 1996) and landscape homogenisation over the period considered might explain its relative decline. *Sylvia undata* is known to depend on higher and denser vegetation on Corsica, where its close relative *Sylvia sarda* is present, than on the continent where *S. sarda* is absent (Martin and Thibault 1996), as we have shown here: the distribution of *S. undata* is linked to the percent cover of medium matorral (plot composition) and to the number of rock or bare soil patches and the total area of medium matorral patches (landscape structure). The temporal changes in vegetation observed on the two islands where this species occurred (Razzoli and Santa Maria) are consistent with the changes in its occurrence. *Monticola solitarius* was mainly related to the percent cover of rock and bare soil (flora variables) in the species distribution analysis. The increase in

percent cover of bare areas on Cavallo (that is buildings and roads in addition to rocks and bare soil) could be part of the explanation because this species breeds in cavities in rocks and walls and forages on roof as well as on rocks (Cramp 1977). On Spargi, where urbanisation was absent and where vegetation became denser, the number of occurrence of this species tended to decrease.

These examples from species for which we have good knowledge on their biology and habitat selection indicate good consistency between species ecology and results from our multi-scale study of their distribution and of their response to change. This suggests that the simultaneous inclusion of different scales can be a powerful tool both to understand patterns but also to help management. Indeed species that vary widely in their response to different scales are likely to respond differently to management regimes. In terms of conservation, spatially limited habitat modifications can be beneficial for species that mainly depend on the local conditions to get established, whereas landscape scale management will be necessary for species that will get established at the local scale only when landscape scale characteristics are right. Having shown the benefits of multi-scale analyses, the challenge remains, however, to be able to identify the response profiles of the different species to be managed, and to design sampling protocols that minimise biases at all scales studied.

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Appendix

Table 5 Recorded bird species in the four islands (number of contacts)

Acronym	Scientific name	Common name	Total		Cavallo		Razzoli		Santa Maria		Spargi	
			1987	2003	1987	2003	1987	2003	1987	2003	1987	2003
PCOL	<i>Phasianus colchicus</i>	pheasant	15	29					15	29		
ACAM	<i>Anthus campestris</i>	tawny pipit	10	2	3	0	5	1	2	1		
TTRO	<i>Troglodytes troglodytes</i>	winter wren	90	61			24	28	37	27	29	6
ERUB	<i>Erithacus rubecula</i>	robin	9	14							9	14
STOR	<i>Saxicola torquata</i>	stonechat	16	0			6	0	9	0	1	0
MSOL	<i>Monticola solitarius</i>	blue rock thrush	16	16	0	3	10	11	1	0	5	2
TMER	<i>Turdus merula</i>	blackbird	48	42			1	0	27	12	20	30
SSAR	<i>Sylvia sarda</i>	marmora's warbler	60	40	1	0	22	21	12	5	25	14
SUND	<i>Sylvia undata</i>	dartford warbler	27	58			1	8	4	12	22	38
SCAN	<i>Sylvia cantillans</i>	subalpine warbler	13	4					0	1	13	3
SMEL	<i>Sylvia melanocephala</i>	sardinian warbler	120	132	19	20	15	23	44	49	42	40
RIGN	<i>Regulus ignicapillus</i>	firecrest	8	0							8	0
MSTR	<i>Muscicapa striata</i>	spotted flycatcher	28	19	2	1	7	0	8	3	11	15
PMAJ	<i>Parus major</i>	great tit	20	20					4	0	16	20
PDOM	<i>Passer domesticus</i>	house sparrow	19	5	9	3	2	0	8	2		
CCHL	<i>Carduelis chloris</i>	greenfinch	32	32	5	6	0	1	18	19	9	6
CCAR	<i>Carduelis carduelis</i>	goldfinch	24	14			2	0	9	4	13	10
CCAN	<i>Carduelis cannabina</i>	linnet	17	21	4	1	8	2	1	4	4	14
ECIR	<i>Emberiza cirius</i>	cirl bunting	8	5					5	5	3	0
		Contacts	580	514	43	34	103	95	204	173	230	212
		Species number	19	17	7	7	12	8	16	14	16	13

Islands are ranked by increasing area. Italic font = species that occur in less than 10% of the census points on each island and that were excluded from the analyses

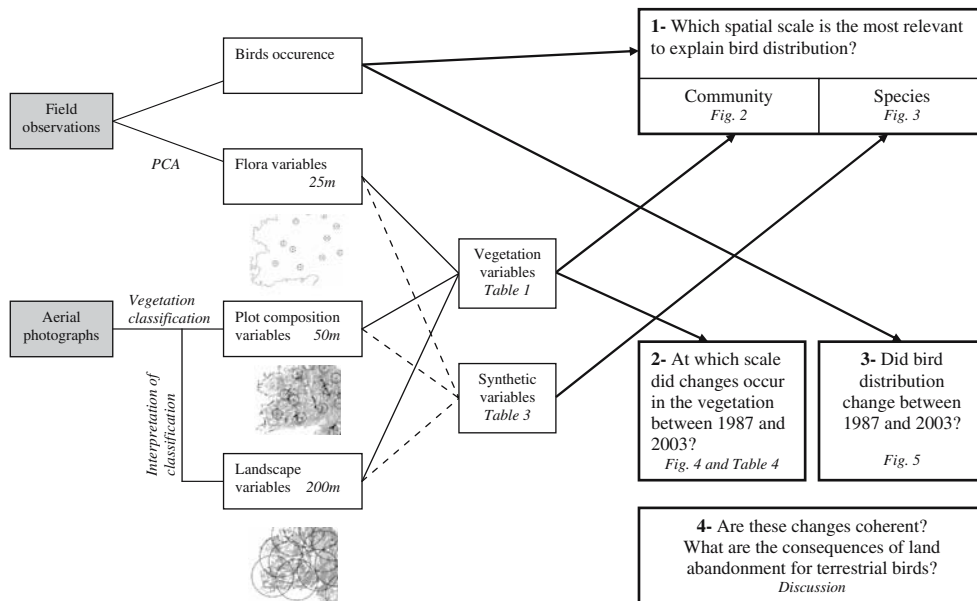


Fig. 6 Flow chart of the variables and their link with questions raised and statistical analyses

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