Does fire increase the spatial heterogeneity of bird communities in Mediterranean landscapes?

SERGI HERRANDO,* LLUÍS BROTONS† & SANTIAGO LLACUNA
Department of Animal Biology (Vertebrates), University of Barcelona, Avenue. Diagonal 645, 08028 Barcelona, Spain

The occurrence of large burnt areas has increased considerably in southern Europe in recent years. In order to design management plans to prevent large wildfires while preserving biodiversity, understanding of the ways in which birds respond to these fires is required. We investigated the spatial variability of both avifauna and habitat structure in three zones: unburnt, burnt in 1982, and burnt in 1994. The habitat structure of the unburnt zone was the most variable spatially. However, bird species composition between sampling points was very homogeneous in space. In contrast, the bird communities inhabiting burnt zones were more spatially heterogeneous. This pattern was caused by distinct specific responses to variations in habitat structure. Open-space species responded to small changes in habitat structure with large changes in local abundance, whereas the response of forest species to these structural variations was much less. We suggest that land managers should select specific zones with limited vegetation recovery within large burnt areas and maintain them as open space to keep combustibility low and provide an appropriate habitat for several open space species that are of conservation concern.

Humans have influenced Mediterranean landscapes for so long that di Castri *et al*. (1981) recognizes a complex 'coevolution' between people and ecosystems. The typical mosaic of Mediterranean landscapes has developed through the effects of human activities such as cultivation, irrigation, livestock grazing, cutting and burning. However, the widespread abandonment of traditional land use in most Euro-Mediterranean regions during the 20th century has led to the growth of extensive and continuous forest and shrubby areas that are very susceptible to fires that can spread rapidly (Blondel & Aronson 1999). Fires can increase landscape heterogeneity by fragmenting continuous blocks of older forest and by initiating local perturbations leading to younger successional stages. However, fires are sometimes so extensive and severe that they reduce structural diversity and homogenize landscape at a regional scale (Trabaud & Galtié 1996, Chuvieco 1999). In

Mediterranean countries fire propagation on abandoned (formerly tilled) land has recently, and rapidly, created a new landscape characterized by huge areas (thousands of hectares) of shrubland with patches of unburnt forests. Present-day management policies aimed at preventing large wildfires are focusing on landscape planning as a way to fight fire. Such policies favour the creation of open areas with little combustible material, which are able to stop the violent progression of wildfires and thus facilitate their control (Hardy & Arno 1996).

The effects on birds of habitat changes resulting from landscape management have been little studied in the Mediterranean Basin (but see Díaz & Martín 1998, Díaz *et al*. 1998, Pons 1998). So far, the effects of fires on Mediterranean bird communities have mostly dealt with the bird species turnover and its close association with the changes in vegetation following a fire (Lawrence 1966, Prodon *et al*. 1984, Stanton 1986, Prodon *et al*. 1987, Pons & Prodon 1996, Izhaki & Adar 1997). However, no studies have focused explicitly on the local-scale spatial variations of bird communities inhabiting extensive shrubby habitats originated by fire.

The main aim of this study was to determine the consequences of large fires on the spatial variability

*Corresponding author.
Present address: Catalan Institute of Ornithology, C./Girona 168, E-5, 08037 Barcelona, Spain.
Email: sherrand@bio.ub.es

†Present address: Centre d'Ecologie Fonctionelle et Evolutive-CNRS, 1919 Route de Mende, 34293 Montpellier Cedex, France

of bird communities. Specifically, we attempt to answer three key questions. Does spatial variability of bird communities differ between burnt and unburnt zones? What is the association between habitat structure and variability of bird communities? Do species that inhabit burnt and unburnt zones respond similarly to changes in habitat structure?

The effects of large fires on biodiversity are of great concern because they represent a major threat to a number of European bird species (Rocamora 1997). Therefore, this study also attempts to develop guidelines for land managers aimed at protecting Mediterranean bird species while preventing large fires.

STUDY AREA

This study was carried out in the Garraf Natural Park, situated 20 km south-west of Barcelona, Spain. The study area (41°15′N, 1°55′E) consists of low hills and small valleys located between 100 and 500 m asl. The mean annual precipitation ranges from 450 to 650 mm, but the karst topography of these hills provides only skeletal soils providing very dry conditions for plant communities. Until now, most studies of the effects of fire on bird communities conducted in the Mediterranean basin have been carried out in areas with acid soils and/or relatively high rainfall. In contrast, our study was undertaken in a dry, karst landscape and thus represents an important contribution to our understanding of avian dynamics after fire in this type of ecosystem.

The area studied was intensively farmed until the end of the 19th century, when the *Phylloxera* crisis almost entirely ruined the vineyards that occupied the hill slopes. There then followed a period of rapid rural depopulation and land abandonment. This allowed the succession of natural plant communities that were only slightly affected by fires. Thus, secondary forests of Aleppo Pine *Pinus halepensis* progressively covered large areas. Traditionally, these forests have been subject to distinct management practices such us cutting the tallest pines and limiting the shrub cover to reduce competition with trees (Vélez 1990). Two extensive fires have profoundly affected the area in recent decades: the first burnt 10 000 ha in 1982 (hereafter called F82) and the second, whose area included that of the first, affected 5000 ha in 1994 (hereafter F94). The north and west of the Park have not been damaged by fire in recent years and here the pines are present everywhere, even in sites where soil is very thin (hereafter called the unburnt zone). The three zones were quite similar in relief and floristic composition, and differed mainly in vegetation structure through the effects of fire (Herrando 2001). Of particular interest was the absence of standing burnt trunks in the two burnt zones. This was because pines burnt in 1982 had already fallen to the ground, and there had been insufficient time for regeneration before the 1994 fire. This is important because the presence of standing dead trees is a strong determinant of post-fire bird succession (Llimona *et al.* 1993).

METHODS

Bird counting

Bird censuses were carried out during the breeding season (March–June) of 1997. The bird-count method was employed to assess the abundance of birds by species. It is also accepted as a suitable way to relate bird abundance to habitat features (Bibby *et al.* 1992). We selected 30 counting stations in each of the three zones (F94, F82 and the unburnt zone), locating them at least 400 m apart to prevent double counting of individuals. We also ensured that the area around each station contained no farmland, urbanized areas or cliffs. Each census was conducted twice. Thus we carried out a total of 180 replicates.

Counting was conducted in the morning, during the period of maximum activity for birds, starting 1 h after dawn, 5 min after the arrival at the station. Point counts taken by other authors have ranged from 5 to 20 min, but following the recommendations of Fuller and Langslow (1984), 10 min was chosen as a compromise. Each bird heard or seen was allocated to one of several concentric bands around the observer but we used all records detected within an unlimited radius. Because all comparisons were made within and not between zones (F94, F82, unburnt), differences in the detectability of species among the three zones are unlikely to affect our analysis. The counting of all birds detected within an unlimited radius was therefore preferred in order to maximize the number of contacts. Abundance indices were obtained for each species by selecting the maximum number of individuals detected in any of the two counts at each station. Raptors, aerial feeders (swallows, swifts and bee-eaters) and crepuscular species were excluded from analysis because this method is not appropriate to assess their abundance (Bibby *et al.* 1992). Censuses were performed by the same observer to avoid interpersonal errors, and

always conducted during good weather conditions, without rainfall or wind.

The number of species or richness was the only direct index used in the analysis. Classical measurements of diversity such as Shannon index H' were not used because they are correlated positively with richness and convey little additional information of Mediterranean breeding bird communities (Prodon 1992).

Vegetation sampling

Habitat characteristics have repeatedly been reported to contribute to the structuring of bird communities (McArthur & McArthur 1961, Willson 1974, Wiens 1989). Specifically, Prodon and Lebreton (1981) showed that habitat structure was the main determinant of bird community structure in Mediterranean shrublands. We therefore decided to use only structural variables as descriptors of habitat, and surveyed the vegetation structure at each bird-count station, following the methodology explained by Prodon and Lebreton (1981). We estimated the cover of distinct vegetation layers (0–0.25 m, 0.25–0.50 m, 0.50–1 m, 1–2 m, 2–4 m, 4–8 m, 8–16 m) and rock layer as habitat variables in an area of about 1 ha around the observer (the few values above zero in the 16–32-m layer were not taken into account in the calculations). Within each layer, the relative cover value was defined as the projection of the foliage volume of the layer (or rock layer) onto a horizontal plane. We estimated this projection by comparison with the reference chart according to Prodon and Lebreton's (1981) procedure. According to these authors, this method produces data that are reliable to ±10%. Cover variables were estimated by the same observer in order to avoid interpersonal errors.

Statistical analyses

Correspondence Analysis (CA) is a descriptive/exploratory technique designed to analyse multiway tables containing some measure of correspondence between the rows and columns (Greenacre 1984, Legendre & Legendre 1998). This type of analysis is especially interesting in the study of relationships between birds and habitats owing to its property of optimization and to the symmetrical role played by the species and the sample stations. CA attributes scores to both species and stations so that the correlation between station scores and species scores is maximal, given the best 'correspondence' between species and stations (Prodon 1992). However, CA is known to cause serious problems such as the edge effect (site scores near the ends of the axes become compressed towards those in the middle) or the arch effect (the parabolic shape of the second axis may make it meaningless in relation to the first, Legendre & Legendre 1998). We have used a modified approach of CA, termed Detrended Correspondence Analysis (DCA), in which detrending by segments and by polynomials corrects the main problems found in CA (Legendre & Legendre 1998). This method allowed us to visualize the degree of aggregation of stations belonging to the three zones studied (F94, F82 and the unburnt) in the factorial space. The stations that are closer correspond to those that tend to have the same bird community and the more scattered are those with lower spatial homogeneity.

After detrending by segments and nonlinear rescaling of the axes, the DCA ordination has the interesting property that the axes are scaled in units of the average standard deviation (sd) of species turnover. Along a gradient, a species appears, rises to its modal value, and disappears over a distance of about 4 sd. Similarly a complete turnover in species composition occurs, over the sites, in about 4 sd. Thus, the length of the first DCA axis is an appropriate measure of the length of the ecological gradient, in species turnover units (Legendre & Legendre 1998). Therefore, the length of the gradient calculated for each of the three zones (F94, F82 and the unburnt zone) was used as a measure of the species turnover within that study zone, which gave us an estimate of the spatial variation of bird communities within each zone.

Another method was used to assess spatial variation in bird composition within each of the studied areas. Zones in which spatial heterogeneity in bird composition is larger, are expected to have smaller mean similarities between sampling stations than those obtained from stations in more homogeneous areas. An index of similarity between each pair of sampling stations was then calculated in each of the study zones. We used Jaccard's index:

$$\text{Jac}\,(x_1, x_2) = a/(a + b + c),$$

where a is the number of species shared by stations x_1 and x_2, b is the number of species observed only in station x_1 and c is the number of species observed only in x_2 (Legendre & Legendre 1998). For each sampling station, we obtained a mean

similarity value calculated by averaging the index of similarity between the focal station and every other sampling station in the study zone (F82, F94 and unburnt).

We also performed a Principal Component Analysis (PCA) for habitat structure, which reduced the number of original variables to uncorrelated synthetic variables. Differences in the variability of scores for each factor between zones were tested by means of Levene's test (Sokal & Rohlf 1995).

In order to discover the relationships between bird species and habitat structure variables we employed generalized linear models (McCullagh & Nelder 1983). For each species, we used its relative abundance as the dependent variable. All abundances followed a Poisson distribution, except for Sardinian Warbler *Sylvia melanocephala*, for which abundance fitted a normal distribution. Therefore, we used different error distributions in each specific model according to the characteristics of the dependent variable. A backward stepwise procedure (P to enter = 0.05, P to remove = 0.10) was conducted to select only significant factors, from the initial set of predictors, that included the first two factors of the PCA carried out with the variables used to describe the habitat features. For each significant association between the abundance of a bird species and any structural factor, we determined the sign of the relationship (positive or negative), and the estimate of the relationship; that is to say, the degree of change in the dependent variable produced by changes in the independent one(s). All statistical analyses were run with STATISTICA (Statsoft Inc. 1999), and CANOCO software.

RESULTS

Bird species richness

In total, 1170 individuals and 36 bird species were recorded during the breeding season, 19 species in F94, 23 in F82 and 25 in the unburnt zone (Table 1). The average richness per station was 6.0 (sd = ±1.8) in F94, 5.6 (sd = ±2.9) in F82 and 11.7 (sd = ±2.9) in the unburnt zone, and differed significantly between the three zones ($F_{2,87}$ = 58.78, $P < 0.0001$). The *post hoc* comparisons of means performed with Newman–Keuls test showed that the unburnt zone showed higher average richness per station than either of the burnt zones ($P < 0.0001$ in both cases), but this parameter did not vary between F82 and F94 ($P = 0.87$).

Bird community structure

The DCA of bird data showed that 21.8% of the total variance was explained by the first factor obtained (DC1), which is a considerable amount given the large data matrix used (36 species). DC1 represented a gradient from birds characteristic of open habitats (negative scores) to forest birds (positive scores, Table 1). Given the characteristics of DCA, it was also possible to rank sampling stations along DC1 according to their species' composition. From this information, there was an obvious overlap of scores between F94 and F82 stations, whereas stations located in burnt zones did not overlap with those of the unburnt zone (Fig. 1). Although point-count ordination showed a continuum from burnt to unburnt habitats, the counting stations situated in the unburnt zone were more clumped than the stations belonging to burnt zones.

In order to quantify differences between zones in the variability of DCA scores without the possible biases associated with the distinct species number per station in each zone, we conducted three separate DCAs, that is, one for each zone (Table 2). The interpretations of the gradients derived from the first factor (DC1) of each group were similar to those found for the DCA performed on the three zones combined (i.e. gradient ranging from open habitat species to closed canopy species). These analyses also showed that the length of the gradient for the first factor was larger in the burnt zones than in the unburnt one (Table 2). Therefore, assuming that this parameter represents a measure of species turnover in stations within the main ordination gradient, F82 and F94 showed greater differences in species composition between the stations located at the ends of the gradient than did the unburnt zone. This was interpreted as burnt zones having more heterogeneous bird communities than the unburnt zone.

In order to check for the consistency of these results, we conducted another analysis, which involved calculating the mean Jaccard's similarity index for the stations of each zone and comparing these values between zones. The mean similarity between stations differed significantly among zones ($F_{2,87}$ = 11.44, $P < 0.0001$). The stations of the unburnt zone showed the greatest similarity, followed by those of F94 and then F82. These differences between the three zones were significant in all cases, as shown by the *post hoc* comparisons (Fig. 2).

Therefore, all these results confirmed that the stations located in the unburnt zone had more similar

Table 1. List of the bird species found. An index of relative abundance was assessed as the mean number of contacts per census station, which are indicated as (abundance in F94, abundance in F82 and abundance in the unburnt zone). The scores for each bird species of the first factor DC1 of the detrended correspondence analysis is also shown.

Bird species	Abundance (F94, F82, unburnt)	DC1
Robin *Erithacus rubecula*	(0.00, 0.00, 0.10)	5.06
Blue Tit *Parus caeruleus*	(0.00, 0.00, 0.03)	4.91
Short-toed Treecreeper *Certhia brachydactyla*	(0.00, 0.00, 0.73)	4.75
Bonelli's Warbler *Phylloscopus bonelli*	(0.00, 0.00, 0.67)	4.69
Coal Tit *Parus ater*	(0.00, 0.00, 0.23)	4.68
Crested Tit *Parus cristatus*	(0.00, 0.00, 0.87)	4.67
Wood Pigeon *Columba palumbus*	(0.00, 0.03, 0.93)	4.57
Magpie *Pica pica*	(0.00, 0.00, 0.30)	4.53
Wren *Troglodytes troglodytes*	(0.00, 0.23, 2.57)	4.47
Jay *Garrulus glandarius*	(0.00, 0.03, 0.63)	4.45
Turtle Dove *Streptopelia turtur*	(0.00, 0.03, 0.67)	4.37
Golden Oriole *Oriolus oriolus*	(0.00, 0.03, 0.40)	4.31
Firecrest *Regulus ignicapillus*	(0.00, 0.10, 0.63)	4.23
Long-tailed Tit *Aegithalos caudatus*	(0.00, 0.13, 0.67)	4.19
Nightingale *Luscinia megarhynchos*	(0.00, 0.23, 1.00)	4.09
Common Cuckoo *Cuculus canorus*	(0.00, 0.10, 0.43)	3.84
Green Woodpecker *Picus viridis*	(0.07, 0.00, 0.50)	3.72
Goldfinch *Carduelis carduelis*	(0.03, 0.03, 0.17)	3.09
Cetti's Warbler *Cettia cetti*	(0.00, 0.10, 0.10)	2.92
Great Tit *Parus major*	(0.13, 0.67, 1.30)	2.85
Blackbird *Turdus merula*	(0.23, 0.80, 1.47)	2.81
Greenfinch *Carduelis chloris*	(0.10, 0.07, 0.40)	2.75
Rock Bunting *Emberiza cia*	(0.03, 0.07, 0.10)	2.63
Serin *Serinus serinus*	(0.33, 0.70, 1.23)	2.49
Sardinian Warbler *Sylvia melanocephala*	(0.97, 2.90, 2.77)	2.34
Dartford Warbler *Sylvia undata*	(2.00, 2.67, 0.00)	1.33
Southern Grey Shrike *Lanius meridionalis*	(0.63, 0.40, 0.00)	0.79
Woodchat Shrike *Lanius senator*	(0.20, 0.00, 0.00)	0.68
Rock Thrush *Monticola saxatilis*	(0.07, 0.03, 0.00)	0.60
Red-legged Partridge *Alectoris rufa*	(1.27, 0.30, 0.00)	0.55
Stonechat *Saxicola torquata*	(0.80, 0.87, 0.00)	0.41
Black-eared Wheatear *Oenanthe hispanica*	(1.47, 0.30, 0.00)	0.25
Ortolan Bunting *Emberiza hortulana*	(0.07, 0.03, 0.00)	−0.17
Thekla Lark *Galerida theklae*	(0.17, 0.07, 0.00)	−0.61
Corn Bunting *Miliaria calandra*	(0.27, 0.00, 0.00)	−0.72
Tawny Pipit *Anthus campestris*	(0.30, 0.03, 0.00)	−1.49

bird communities than those located in burnt zones, which showed spatially variable bird assemblages.

Habitat structure

The first two factors of the correspondence analysis performed with the structural data accounted for 60.86% of the total data matrix variance (Table 3). The first factor (SF1) was correlated with all the variables, from the most negative (rocks) to the most positive (trees). This factor can therefore be interpreted as a gradient of increasing structural complexity, closely related to fire influence. The second structural factor (SF2) was negatively correlated with large trees and very small plants (herbs or small ligneous plants less than 25 cm tall) and positively with shrubs. Thus, SF2 represented a gradient of shrub development rather than that of trees or small plants. Shrub layers are absent both from recently burnt sites and from many Iberian forests, which are commonly managed to limit the growth of shrubs (López & Moro 1997). An obvious but noticeable point was that F94 had the fewest vegetation layers whereas the unburnt zone had the highest. The unburnt zone showed significantly greater variance in structural factors than F94 (Levene's test $F_{1,58} = 50.32$, $P < 0.0001$ for SF1 and Levene's test $F_{1,58} = 13.47$, $P < 0.001$ for SF2) (Fig. 3). The first structural
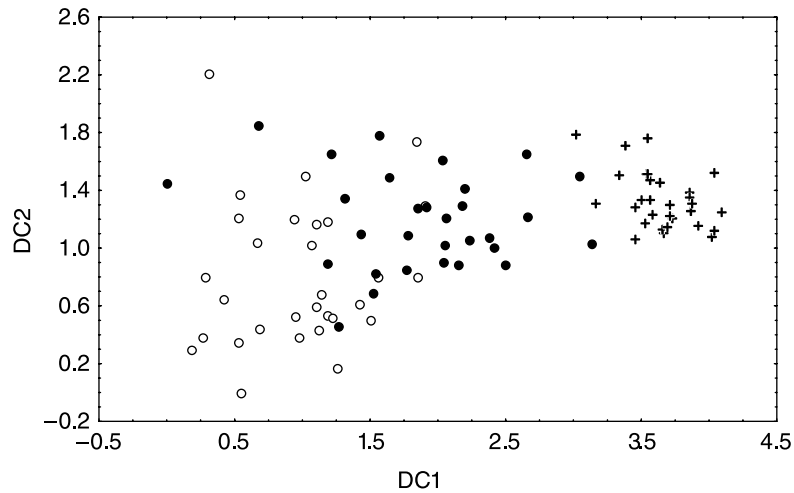
Figure 1. Projection of the 90 bird counting stations on the plane defined by the first two factors (DC1 and DC2) of the detrended correspondence analysis of breeding bird communities, north-eastern Spain. Open circles, mean F94 stations; solid circles, F82 stations; crosses, unburnt stations.

Table 2. Results of the DCA carried out for all zones together and for each zone separately. Main parameters from the first factor (DC1) are shown, as well as the inertia of the analysis including all factors.

|	DCA for all zones	DCA for F94	DCA for F82	DCA for the unburnt
DC1 Eigenvalue	0.681	0.293	0.377	0.183
DC1% variation explained	21.8	15.7	15.7	15.5
DC1 Length of the gradient	4.091	2.419	3.634	1.829
Total inertia	3.12	1.87	2.40	1.17
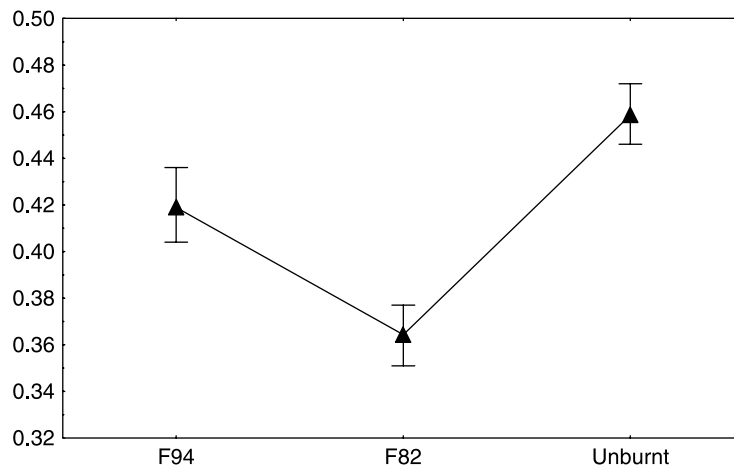
Figure 2. Mean and se for the index of similarity among stations in each zone. We calculated for each sampling station the mean value of Jaccard similarity indexes with each other sampling station for each study zone. The results of the *post hoc* Newman–Keuls test show differences among all groups: $P < 0.01$ for the comparison between F94 and F82, $P < 0.05$ for the comparison between F94 and the unburnt zone, and $P < 0.001$ for the comparison between F82 and the unburnt zone.

Table 3. Correlations between the relative cover of each structural layer (vegetation layers and rock layer) and the first two factors of the Principal Component Analysis carried out with structural data (SF1 and SF2).

	SF1	SF2
Rock percentage	−0.65***	0.02
0.00–0.25%	−0.45***	−0.64***
0.25–0.50%	−0.27**	0.50***
0.50–1.00%	0.71***	0.58***
1.00–2.00%	0.84***	0.21*
2.00–4.00%	0.77***	−0.10
4.00–8.00%	0.65***	−0.56***
8.00–16.00%	0.59***	−0.49***
Eigenvalues	3.27	1.59
% Variation explained	40.92	19.94

***$P < 0.001$, **$P < 0.01$, *$P < 0.05$.
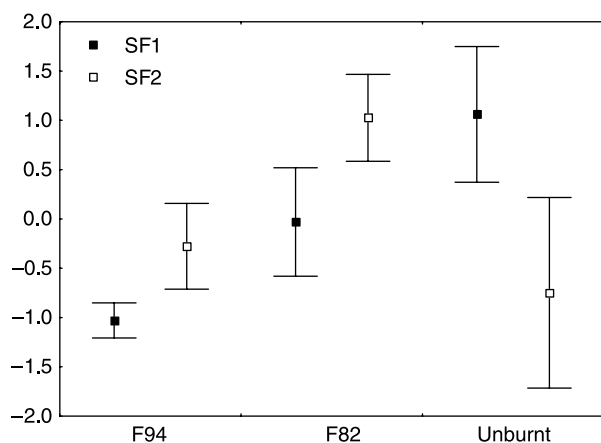
Figure 3. Mean and sd for structural factors (SF1 and SF2) in F94, F82 and the unburnt zone.

factor (SF1) was also more variable in F82 than in F94 (Levene's test $F_{1,58} = 21.64, P < 0.0001$), although no difference was found between these two zones for SF2 (Levene's test $F_{1,58} = 0.003, P = 955$) (Fig. 3). Finally, the unburnt zone showed significantly greater variance than F82 for SF2 (Levene's test $F_{1,58} = 13.12, P < 0.001$) but the difference was only marginal for SF1 (Levene's test $F_{1,58} = 3.47, P = 0.067$) (Fig. 3). Therefore, the spatial variation of structural factors, which is commonly reported to induce variations in bird communities, was greater in the forested than in the more open areas. However, there is an apparent contradiction with the results of the DCA performed with birds, which showed the greatest spatial variability of bird communities in the burnt zones and the least in the unburnt one.

Bird–habitat structure relationship

The first factor of the DCA performed with birds (DC1), which was interpreted as a gradient from birds of open habitats to birds of woody habitats according to the ecology of the species, was correlated positively with the structural complexity (SF1) ($r = 0.80$, $P < 0.0001$). This result supported the previous interpretation of DC1.

We used generalized linear models to quantify the bird response to changes in habitat features (Table 4). Out of the 36 bird species found in the study, 30 had models that included SF1, whereas SF2 was only included in the models for 15 species. A positive relationship between abundance and a gradient of increasing structural complexity (SF1) was found in 21 species, whereas only in nine species was abundance negatively related to SF1. The estimate or coefficient of each relationship between bird species abundance and structural factors is represented by the slope of the equation, so that high values of these estimates indicate high variation in bird abundance when habitat structure changes. For the set of species positively related to SF1, the mean absolute estimate (which was 0.77) was significantly lower ($t_{28} = -5.25$, $P < 0.0001$) than that of the set of the species that were negatively related to SF1 (which was 1.95). Therefore, small variations in SF1, which represented a gradient of structural complexity, induced greater effects in the abundance of species that were associated negatively with this structural factor than in the abundance of the species associated positively with it.

DISCUSSION

Helle and Mönkkönen (1990) suggested that, for many types of ecosystems, the relative growth rate of vegetation often reaches its peak during the intermediate stages of forest succession and is associated with a rapid change in bird communities. In Mediterranean landscapes, Prodon (1992) showed that in the transition between shrubland and forest stages any variation in the tree/shrub ratio was sufficient to induce noticeable changes in the avifaunal composition associated with a rapid increase in bird diversity. According to this author, it may be caused by the presence of patchy vegetation at this stage, when bushes and scattered young trees coexist for several years before canopy closure. These transitions are composed of assemblages of forest and open landscape bird species resulting from a shortage of

Table 4. Generalized linear models using the abundance of each bird species as dependent variable. A backward step-wise procedure (*P* to enter = 0.05, *P* to remove = 0.10) was conducted to select only significant factors from the initial set of predictors that included the two main factors of the correspondence analyses performed with structural variables (SF1 and SF2). All dependent variables followed a Poisson distribution, except for Sardinian warbler *Sylvia melanocephala*, whose abundance fitted a normal distribution. Species are ordered according to the scores of the parameter with SF1.

Species	Intercept	SF1	SF2	χ^2	df	P
Robin *Erithacus rubecula*	−4.18**	1.2[a]		4.46	1	0.034
Wood Pigeon *Columba palumbus*	−2.22***	1.13***	−0.82***	54.5	2	<0.0001
Crested Tit *Parus cristatus*	−1.98***	1.09***		32.1	1	<0.0001
Jay *Garrulus glandarius*	−2.42***	1.08***	−0.67*	33.3	2	<0.0001
Coal Tit *Parus ater*	−3.27***	1.03**		7.65	1	0.005
Short-toed Treecreeper *Certhia brachydactyla*	−2.11***	1.00***	0.50**	28.5	2	<0.0001
Golden Oriole *Oriolus oriolus*	−2.55***	0.87**	−0.57*	15.1	2	0.001
Wren *Troglodytes troglodytes*	−0.58***	0.86***	−0.40***	83.0	2	<0.0001
Firecrest *Regulus ignicapillus*	1.93***	0.84***	−0.46*	21.9	2	<0.0001
Bonelli's Warbler *Phylloscopus bonelli*	−2.35***	0.83***	0.86***	31.3	2	<0.0001
Turtle Dove *Streptopelia turtur*	−1.89***	0.81***		15.0	1	<0.0001
Long-tailed Tit *Aegithalos caudatus*	−1.72***	0.71***	−0.45*	19.0	2	<0.0001
Magpie *Pica pica*	−3.14***	0.70[a]	−0.95***	14.7	2	<0.0001
Common Cuckoo *Cuculus canorus*	−2.07***	0.68**		8.2	1	0.004
Green Woodpecker *Picus viridis*	−2.28***	0.64**	−0.79**	21.5	2	<0.0001
Nightingale *Luscinia megarhynchos*	−1.19***	0.62***	−0.39**	22.3	1	<0.0001
Greenfinch *Carduelis chloris*	−1.92***	0.55*		5.8	1	0.016
Great Tit *Parus major*	−0.52**	0.54***		20.3	1	<0.0001
Serin *Serinus serinus*	−0.37**	0.36**		9.9	1	0.002
Blackbird *Turdus merula*	−0.49*	0.32***		20.2	1	<0.0001
Sardinian Warbler *Sylvia melanocephala*	0.76***	0.26***	0.14*	27.1	2	<0.0001
Dartford Warbler *Sylvia undata*	−0.11	−0.91***	0.93***	114.6	2	<0.0001
Southern Grey Shrike *Lanius meridionalis*	−1.48***	−1.01**		16.7	1	<0.0001
Stonechat *Saxicola torquata*	−1.08***	−1.11***	0.43*	34.1	2	<0.0001
Red-legged Partridge *Alectoris rufa*	−1.23***	−1.27**		35.9	1	<0.0001
Black-eared Wheatear *Oenanthe hispanica*	−1.37***	−1.59***		53.3	1	<0.0001
Woodchat Shrike *Lanius senator*	−4.60**	−2.42*		10.1	1	0.002
Thekla Lark *Galerida theklae*	−3.56**	−2.73**		4.71	1	0.029
Tawny Pipit *Anthus campestris*	−5.12***	−3.16**	−1.31*	24.4	2	<0.0001
Corn Bunting *Miliaria calandra*	−5.37**	−3.32*		16.8	1	<0.0001

***$P < 0.001$; **$P < 0.01$; *$P < 0.05$; [a]$P < 0.1$.

species specific to intermediate successional stages. Although a few F82 stations (15 years after fire) were close to the unburnt ones, most of the bird communities at these stations consisted of species typical of shrubby habitats, thus indicating that they have not achieved the transitional stage reported by Prodon (1992). According to the habitat structure of these stations, this period of rapid turnover may coincide with the moment when trees reach 4 or 5 m in height.

At a regional level, Blondel and Farré (1988) showed that in Europe, forest bird communities in different areas were very similar, whereas those of open habitats differed significantly. These authors pointed out that open or semi-open habitats were subjected more directly to local environmental factors than were forests, in which conditions were largely buffered by the habitat structure. Our results show a comparable pattern at a smaller scale, because the bird communities inhabiting the unburnt forested zone were spatially more uniform than those inhabiting open or semi-open burnt zones. Structural changes in this Mediterranean forest produced little variation in the bird community. In contrast, the bird communities of zones affected by fire were largely determined by small changes in habitat structure. Within the two zones disturbed by fire, burnt either 15 or 3 years before the fieldwork, the bird communities inhabiting the former were the more variable spatially. As mentioned above, this zone contained some stations with young trees sticking out up to 5 m from a dense and tall shrub layer and thus contained a bird community quite similar

to the unburnt zone. Nevertheless, in other F82 stations the vegetation was mainly lower than 50 cm tall (very few Aleppo Pines exceeded this height, and the tallest of these was 1.5 m). These notable differences in vegetation development may be associated directly with soil depth. Soil heterogeneity may also be found in the zone burnt in 1994, but here the time elapsed since fire had not been sufficient to allow the growth of vegetation in sites with adequate soil. Therefore, our results suggest that, in this study area, fire increases the spatial variability of bird communities; however, this happens to a greater degree in areas burnt 15 years before than in areas burnt more recently, i.e. variability increases with time since a fire.

The variability of habitat structure showed the opposite pattern to that shown by bird communities. In fact, the habitat structure was spatially most variable in the unburnt zone. In the main, this was probably caused by two factors: a greater variability intrinsic to a system with more vegetation layers, and the presence of forest management practices carried out with different intensity. However, this variability did not induce a strong turnover in species composition among stations located in forested areas. Thus, the mere presence of adult Aleppo Pines implied the appearance of forest bird communities, which were highly shaped by the presence of these trees but were not much influenced by the variability within the forest vegetation layers, at least compared with the postfire communities. López and Moro (1997) found that the composition of bird communities in Aleppo Pine forests of south-eastern Spain was better explained by understorey characteristics than by the tree layer. Even taking into account the fact that unburnt stations differed in the intensity of tree and understorey management, our results show that changes in habitat structure affected the bird assemblages of these forests to a lower degree than those of the zones affected by fire.

We found that bird species living in burnt zones responded to changes in habitat structure significantly more than did forest species. These results indicate that forest birds were very resilient to the changes in habitat features whereas birds inhabiting burnt zones were influenced strongly by small variations in the few layers present in shrubby vegetation. This is why small differences in the habitat structure of burnt zones resulted in large differences in bird communities, whereas the high degree of spatial variability in forest structure hardly influenced bird communities.

Management considerations for bird conservation

This work shows that the apparent effects of large fires on bird diversity depend on the scale at which they are considered. We found more bird species at unburnt stations than at those of either burnt zone. Thus, at this small scale, large fires may be seen as harmful for forest bird diversity. However, the variability of bird communities among the unburnt stations was much less than it was among the stations of F94 or F82 and, as a consequence, bird total richness was greater in the burnt zones. In fact F82, taken as a whole, had almost as many bird species as the unburnt zone. These results therefore emphasize the importance of the multiscale approach, used increasingly by ecologists in recent years (Wiens 1994, Jokimäki & Huhta 1996, Drapeau *et al.* 2000).

Burnt zones have been reported as interesting areas in terms of overall biodiversity conservation (Blondel & Aronson 1999). Only four of the species that inhabited the unburnt area (16%) are considered under conservation priority A, B, or C with regards to the particular importance of habitat for their survival (Rocamora 1997). In contrast, 12 species inhabiting burnt zones (46%) fall within this conservation category. These results magnify the biological value of maintaining burnt areas as well as forested areas. Fires in very dry areas, such as the Iberian Mediterranean coast, may create habitats that are appropriate for the maintenance of many bird species of conservation priority. Therefore, in spite of the general view of these areas as poor habitat with a slow rate of vegetation recovery, they may make a significant contribution to the conservation of some of the most threatened bird species in Europe.

Our results also suggest that, within the burnt areas, the bird community at any site tends to be distinct from that at another. Because many bird species belonging to Conservation Priority A, B, or C (Rocamora 1997) inhabit burnt zones with very small shrubs, conservation action might be better focused on determining the specific zones required. Zones that even several years after fire are still dominated by small shrubs, offer the best habitat for open-space species because these areas are the most resistant to successional processes, and so may support populations of these birds for longer. Often these zones are affected by frequent fires. This might allow bird species of interest to remain for decades. But in other cases this natural disturbance is not frequent enough and succession finally proceeds. Here,

management should be undertaken to enhance bird diversity and maintain open areas with little vegetation in order to avoid the violent advance of large and catastrophic wildfires.

One of the easiest ways to control the growth of plants might be prescribed burning. This is now a widely used management tool that can help to prevent large-scale catastrophic wildfires (Hardy & Arno 1996, Miller & Urban 2000). Prescribed burning usually has a relatively modest impact on bird communities (Bock & Bock 1983, Petersen & Best 1987, Pons 1998, but see Robertson & Jarvis 2000). In Mediterranean France, Pons (1998) found that after a prescribed fire that burned 76% of a 8.25-ha plot, high priority bird species such as Tawny Pipit *Anthus campestris* and Wood Lark *Lullula arborea* increased their densities, whereas other priority species of Mediterranean habitats, such as Sardinian Warbler *Sylvia melanocephala* and Dartford Warbler *Sylvia undata*, had enough shrubs to remain after the fire. Our results also show that the abundance of bird species of high conservation priority responds strongly to small changes in vegetation structure and that these changes happen at a small scale; this scale coincides approximately with the area required for a prescribed burn in order to prevent large wildfires.

Increased grazing by means of the reintroduction of large herbivores or livestock husbandry is another strategy that can be used to limit vegetation growth in burnt areas. Livestock grazing is often considered to be detrimental to bird communities (Bock & Bock 1999, Fuller & Gough 1999), but one of the few studies carried out in the Mediterranean basin has reported positive effects for maintaining several Priority European bird species (Pulido & Díaz 1992). We recommend that management (prescribed burning, grazing or any other management technique suitable to remove vegetation) be concentrated in specific burnt zones to minimize biomass accumulation, maintain fire breaks, and conserve the bird community of open spaces.

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