

## Forest bird diversity in Mediterranean areas affected by wildfires: a multi-scale approach

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Fire is a key mechanism creating and maintaining habitat heterogeneity in Mediterranean landscapes by turning continuous woody landscapes into mosaics of forests and shrublands. Due to the long historical role of fires in the Mediterranean, we hypothesised a moderate negative effect of this type of perturbation on forest bird distribution at a landscape level. We conducted point bird censuses in Aleppo pine forest patches surrounded by burnt shrublands and studied the relationships between three ecological groups of bird species (forest canopy species, forest understorey species, and ubiquitous species) and the features of local habitat, whole patch and surrounding landscape. We used a multi-scale approach to assess the effects of landscape variables at increasing spatial scales on point bird richness. Regarding local habitat components, canopy species were positively associated with tall pines while understorey species with the cover of shrubs and plants from holm-oak forests. Forest birds were positively related to patch size and irregular forest shapes, that is, with high perimeter/size ratios. Thus, these species did not seem to perceive edges as low quality but rather favourable microhabitats. We did not detect any negative effect of isolation or cover of woodlands in the landscape on the presence of forest species after local habitat factors had been accounted for. Finally, only local habitat factors entered the model for ubiquitous species. We suggest that mosaic-like landscapes shaped by fires in the Mediterranean basin are not strongly associated with negative effects fragmentation on forest birds other than those related with habitat loss.

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Habitat fragmentation consists of the subdivision of a continuous habitat into smaller pieces, thereby altering the landscape structure through a loss of a given habitat and changes in the spatial configuration of remnant patches (Saunders et al. 1991, Andrén 1994). Several studies have found that forest fragmentation has deleterious consequences for forest birds, but these have been basically carried out in landscapes directly modified by human activities such as farming (e.g. Bellamy et al. 1996, Díaz et al. 1998, Tellería and Santos 1999), timber exploitation (e.g. Askins et al. 1987, Jokimäki and Huhta 1996, Schiemegelow et al. 1997) or urbanisation (e.g. Friesen et al. 1995, Mancke and Gavin 2000), and data for landscapes where forests have been frag-

mented by natural disturbances such as fires are scarce. The historical background of the first three types of fragmentation differed notably from that associated with fire-shaped landscapes, possibly inducing different responses of vertebrates to landscape structure (Mönkkönen and Reunanen 1999). Man-induced fragmentation associated with processes such as farming or logging are historically recent (but see Mönkkönen and Welsh 1994) whereas fire is a natural disturbance involved in the dynamics of many ecosystems (Kozłowski and Ahlgren 1974).

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shrubby matrix (Forman 1995). Fire has lost part of its historical role in many developed countries as a result of present landscape management and fire-control policies (Hunter 1993). In contrast, current land abandonment in Euro-Mediterranean countries has led to the encroachment of formerly cultivated lands by woody vegetation (Preiss et al. 1997) which, together with a general climate trend towards drier and warmer conditions (Piñol et al. 1998), has greatly contributed to increasing the extent of burnt areas in recent decades. However, fire-induced forest fragmentation cannot be considered a recent process but rather a phenomenon which is intrinsically linked with the dynamics of Mediterranean ecosystems that humans have enhanced during their long-lasting activity in the Mediterranean Basin (Trabaud 1981, Blondel and Aronson 1999). The study of the effects of fires on Mediterranean bird communities has focused on the successional dynamics of burnt areas itself (e.g. Lawrence 1966, Prodon et al. 1987, Pons and Prodon 1996, Izhaki and Adar 1997). Nevertheless, no attempt has been made to study the consequences of the fire regime at a landscape level on the bird assemblages inhabiting forests fragments within a burnt matrix.

If the land transformation provoked by natural disturbances such as fire has been incorporated into the habitat selection processes of forest bird species, we expect that, apart from habitat loss, this type of landscape change will cause hardly any negative impacts on Mediterranean forest birds. Specifically, we address the following questions: what are the independent effects of local habitat, whole patch and landscape structure on bird assemblages in landscape mosaics generated by fire? Are bird communities negatively affected by habitat loss and the concomitant increase in edges? Is the shrubby matrix permeable enough to reduce the effects

of patch isolation on forest birds? Given that burnt habitats are dominated by shrubs, we also predict that forest species foraging in the shrubby understory will be less affected by forest fragmentation than forest canopy species.

## Methods

### Study area

Fieldwork was carried out in the coastal mountains located between Barcelona and Tortosa cities, in the northeast of the Iberian Peninsula (41°N, 1°E, Fig. 1). The study area ranges from 100 to 700 m a.s.l. and is located between the mesic "meso-Mediterranean" and the xeric "thermo-Mediterranean" life zone. The first is characterised by closed canopy holm-oak *Quercus ilex* forests, whereas the second, is dominated by dense, low height, coastal shrublands of wild olive tree *Olea europaea*, lentisk *Pistacia lentiscus* and Mediterranean dwarf palm *Chamaerops humilis* among others (Blondel and Aronson 1999). These two types of vegetation were formerly dominant in the landscape but, like many other areas of the Mediterranean Basin, the original landscape was changed by human activity several millennia ago and since then it has undergone continuous redesign. The mountains of the study area were heavily cultivated until the beginning of twentieth century. From then on, it has started a progressive depopulation of most rural areas that has allowed the recovery of secondary natural vegetation. Today, secondary low shrubby formations (Rosmarino-Ericion) and Aleppo pine *Pinus halepensis* forests have dominated the landscape. These formations are prone to affection by wildfires, which burn large areas in the Mediterranean Basin periodically. In forest areas dominated by Aleppo

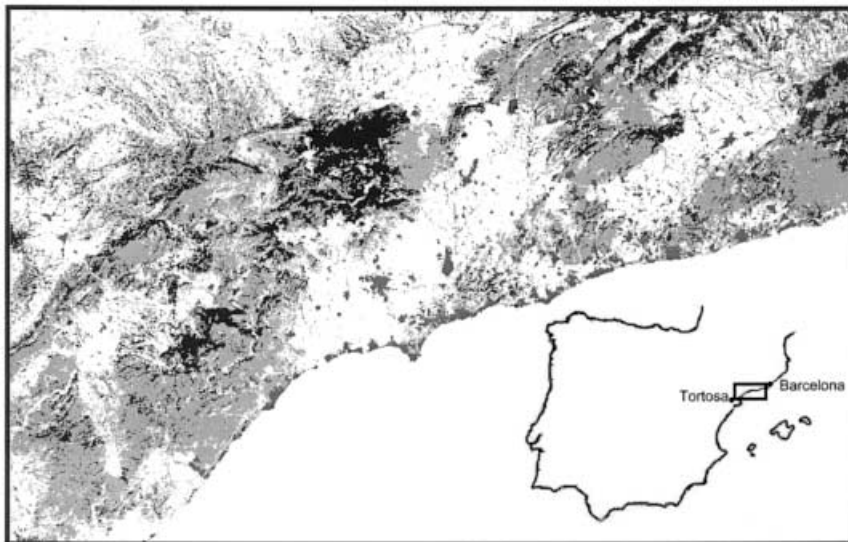


Fig. 1. Geographic location and vegetation map of the study area based on a Landsat satellite image. Black zones represent forests, soft grey represent shrublands burnt in last decades, dark grey represent urbanised areas and white zones represent farmland. A high component of forest fragmentation due to fires can be easily appreciated in this image.

pinus, wildfires kill the trees and burn completely the aerial parts of shrub. However, because most of shrub species sprout from unaffected roots, fires fragment forests by creating a burnt, very dense and low matrix (Trabaud 1981). In case of recurrent fires, Aleppo pine, which is not a sprouting species, is not able to grow enough to reproduce and shrubby areas evolve towards a more permanent shrubland without a tree layer. The study area was characterised by the presence of remnant Aleppo pine forests, which were aggregated or isolated to a variable degree, and surrounded essentially by a burnt shrubby matrix.

### Study design

By means of aerial photographs (1:25 000, Institut Cartogràfic de Catalunya 1993 and 1997) we searched for forest patches surrounded by a burnt shrubby matrix. For the present study, we selected 36 of these forest patches (mean = 52.7 ha, SE = 16.6, ranging from 0.4 to 311 ha) which were accessible to the observers in preliminary field visits. Forest patches were also selected so that a minimum distance between them was 2 km to ensure independence in the landscape characteristics surrounding each one.

We used a multi-scale approach (Wiens 1989, 1994, Andrén 1994, Jokimäki and Huhta 1996, Saab 1999, Drapeau et al. 2000) which assessed the effects of landscape structure (composition and configuration) and patch characteristics after controlling for local habitat effects (structure and floristics) on forest bird occurrence.

The analysis of animal assemblages in relation to patterns at distinct spatial scales requires the control of the effects exerted by the variables at each scale, since they can be correlated. This could be done a priori, with an experimental design that controls the variation of the smaller scales (Donovan et al. 1997), although this is not always feasible in real landscapes (Drapeau et al. 2000). Therefore, we decided to control a posteriori for the effect of including variables at different scales by progressively removing the effect of smaller scale variables. We assumed that explained variation shared by variables at different spatial scales is linked to the one operating at the smallest scale. Therefore, we considered that breeding bird occurrence was affected first by the local habitat, then by forest patch characteristics and finally by landscape surroundings. We are aware that our approach is conservative in relation to landscape effects on bird distribution because shared variance across different scales would be attributed to smaller scales. However, given the complexity of landscape related effects on bird ecology and distribution, we think that such approaches are necessary to identify significant landscape effects which are independent of small scale habitat characteristics (Buckland and Elston

1993). The inclusion of different scale variables at one step often results in the selection by statistical models of "summary predictors", that is, predictor variables that better summarise landscape characteristics across scales but which are not necessarily associated with functional processes acting at given spatial scales.

Bird occurrence was measured by means of census point counts at the selected forest patches. We located one census point in the centre of each forest patch, in which we also measured local vegetation characteristics (local scale). Then the spatial characteristics of the forest patch (forest patch scale) in which the bird point count was located were measured. And finally, we also measured the landscape structure (landscape scale) in 4 km<sup>2</sup> (2 × 2 km) squares centred at each of the bird point counts conducted. Using this method we are able to assess how bird occurrence was related to the characteristics of the surrounding habitat at increasing spatial scales.

### Bird censuses

The point-count method (Bibby et al. 1992) was used to determine the species that breed in the forest patches (for similar procedure see Jokimäki and Huhta 1996, Saab 1999). We conducted two bird censuses in each forest patch during the breeding season in 2000, the first from March to April and the second from May to July. The presence of species within a 50-m radius of the count station was recorded during 20 min. The census time was long to maximise the probability of detecting breeding bird species (Drapeau et al. 1999). Censuses were made in the period of maximum bird activity, from dawn to 3 h later, and they were not conducted in adverse weather conditions such as rain or strong wind.

Raptors, owls and nightjars were not reliably detected with our census technique (Bibby et al. 1992) and were therefore excluded from the analyses. Some of the species detected did not breed at all in the fragments, either because they nested in open areas and visited forests only occasionally, or because they were late-season migrants that did not breed in the area. Some other species records from the smallest fragments could be attributable to transient individuals breeding in some other forested areas nearby (Hinsley et al. 1995, Díaz et al. 1998). To avoid this potential bias, such records were considered only when direct breeding evidence was obtained in the forest fragment (e.g. nest construction or provisioning behaviour) or when the species was detected on two visits (for a description of a similar procedure see Díaz et al. 1998).

Monitoring specific preferences in habitat use is most revealing if birds are grouped by habitat use strategies (Järvinen and Väisänen 1979). Mediterranean forests usually have a developed shrub layer, which implies

Table 1. The bird species found breeding in Aleppo pine forest in the study area. Species were classified as forest canopy (CA), forest understorey (UN) and ubiquitous (UB) according to their ecological preferences during breeding season (see Methods). The percentage of bird point counts where each species was found is also shown.

| Bird species  | Ecological group | % point counts occupied |
|---|------------------|-------------------------|
| <i>Sylvia melanocephala</i> Sardinian warbler       | UN               | 100.0                   |
| <i>Turdus merula</i> blackbird                      | UN               | 88.9                    |
| <i>Serinus serinus</i> serin                        | UB               | 77.8                    |
| <i>Parus major</i> great tit                        | CA               | 75.0                    |
| <i>Columba palumbus</i> wood pigeon                 | UB               | 72.2                    |
| <i>Parus cristatus</i> crested tit                  | CA               | 66.7                    |
| <i>Certhia brachydactyla</i> short-toed treecreeper | CA               | 63.9                    |
| <i>Troglodytes troglodytes</i> wren                 | UN               | 58.3                    |
| <i>Luscinia megarhynchos</i> nightingale            | UN               | 55.6                    |
| <i>Phylloscopus bonelli</i> Bonelli's warbler       | CA               | 47.2                    |
| <i>Cuculus canorus</i> common cuckoo                | UB               | 41.7                    |
| <i>Oriolus oriolus</i> golden oriole                | UB               | 38.9                    |
| <i>Carduelis chloris</i> greenfinch                 | UB               | 38.9                    |
| <i>Aegithalos caudatus</i> long-tailed tit          | CA               | 36.1                    |
| <i>Garrulus glandarius</i> jay                      | CA               | 36.1                    |
| <i>Carduelis carduelis</i> goldfinch                | UB               | 36.1                    |
| <i>Streptotelia turtur</i> turtle dove              | UB               | 33.3                    |
| <i>Eritacus rubecula</i> robin                      | UN               | 33.3                    |
| <i>Picus viridis</i> green woodpecker               | UB               | 27.8                    |
| <i>Regulus ignicapillus</i> firecrest               | CA               | 27.8                    |
| <i>Lullula arborea</i> woodlark                     | UB               | 22.2                    |
| <i>Sylvia atricapilla</i> blackcap                  | UN               | 16.7                    |
| <i>Muscicapa striata</i> spotted flycatcher         | UB               | 16.7                    |
| <i>Lanius senator</i> woodchat shrike               | UB               | 19.4                    |
| <i>Parus caeruleus</i> blue tit                     | CA               | 13.9                    |
| <i>Emberiza cirrus</i> ciril bunting                | UB               | 13.9                    |
| <i>Hippolais polyglotta</i> melodious warbler       | UN               | 11.1                    |
| <i>Passer domesticus</i> house sparrow              | UB               | 11.1                    |
| <i>Jynx torquilla</i> wryneck                       | UB               | 8.3                     |
| <i>Parus ater</i> coal tit                          | CA               | 8.3                     |
| <i>Emberiza cia</i> rock bunting                    | UB               | 8.3                     |
| <i>Miliaria calandra</i> corn bunting               | UB               | 5.6                     |
| <i>Turdus viscivorus</i> mistle thrush              | UB               | 2.8                     |
| <i>Sylvia cantillans</i> subalpine warbler          | UN               | 2.8                     |
| <i>Phylloscopus collybita</i> chiffchaff            | CA               | 2.8                     |
| <i>Carduelis cannabina</i> linnet                   | UB               | 2.8                     |

that a significant proportion of Mediterranean bird species is adapted to shrubby forests (Tellería and Santos 1999). Another common feature of Mediterranean forests is a high degree of heterogeneity and habitat variation from which generalists or ubiquitous species benefit (Blondel and Aronson 1999).

According to specific dependence on forest habitats for breeding and foraging activities described in the literature (Perrins 1998), we classified the species into two main groups: forest species (species that require forest habitat for both breeding and foraging) and ubiquitous species (species that can use alternative habitats, such as open fields for foraging or breeding). Forest species were in turn grouped into canopy and understorey species, depending on the forest stratum in which they concentrate their activity. Thus, among the canopy species we included tits, arboreal warblers such as the *Phylloscopus bonelli* and *Regulus ignicapillus*, and *Certhia brachydactyla*. Among understorey species we included *Troglodytes troglodytes*, thrushes such as *Turdus merula* and *Luscinia megarhynchos*, and shrubby warblers such as *Sylvia melanocephala* and *Hippolais*

*polyglotta*. Finally, among the ubiquitous species we included birds such as *Lullula arborea*, *Muscicapa striata*, pigeons, finches and buntings. Woodpeckers such as *Picus viridis* and *Jynx torquilla* were included in this latter group because in the Mediterranean these species are not only found in forests but also in almond or olive tree crops, and in isolated burnt trunks (Table 1).

### Local habitat structure and floristics

The floristic and structural features of forests usually synthesise the set of local habitat requisites of forest birds (Robinson and Holmes 1984). Therefore, we sampled the local habitat structure and floristic composition around each bird point count within a 50-m radius around the observer. To characterise habitat structure, we estimated the cover of bare ground, the cover of several vegetation layers (0–0.25 m, 0.25–0.5 m, 0.50–1 m, 1–2 m, 2–4 m, 4–8 m, 8–16 m, > 16 m), the maximum vegetation height and the number of adult pines in 100 m<sup>2</sup> as habitat structure variables. Within

each vegetation layer, relative cover value was defined as the projection of the foliage volume of the layer on a horizontal plane. This was estimated by comparison with a reference chart, following the procedure described by Prodon and Lebreton (1981).

We also estimated the relative cover of understorey plant species following the same procedure. Plant species were grouped according to the phytosociologic criteria shown by Folch (1986) for the eastern Iberian Peninsula. Four main groups were made. First, plants belonging to secondary low shrubland formations on calcareous soils (Rosmarino-Ericion), such as *Rosmarinus officinalis*, *Erica multiflora* or *Ulex parviflorus*. Second, plants belonging to primary dense tall shrublands (Oleo-Ceratonion), such as *Olea europaea*, *Pistacia lentiscus*, *Chamaerops humilis* or *Quercus coccifera*. Third, plants belonging to primary holm-oak forest (*Quercion ilicis*), such as *Quercus ilex*, *Rhamnus alaternus* or *Smilax aspera*. Finally, the fourth group was made up of grasses such as *Brachypodium* sp. or *Ampelodesmos mauritanica*, which are often associated with highly disturbed lands. For each bird point count, we obtained an abundance index for each phytosociological group by summing the cover of plants belonging to each one.

### Forest patch variables

Patch characteristics could influence animal populations in fragmented landscapes (Fahrig and Merriam 1994). To analyse the effects of patch characteristics on bird assemblages, we used digitised aerial photographs (1:25 000) to construct IDRISI image files using the program MiraMon GIS (Marcer and Pons 1998). The images were then analysed with FRAGSTATS software (McGarigal and Marks 1995) to obtain patch metrics. Forest shape measures the perimeter<sup>2</sup>/size ratio of a particular patch, high values of the index being those that correspond to irregular forest shapes. Core area is defined as the area within a patch beyond a given distance from the edge. In this study, following Murcia (1995), we considered that the distance from the edge to avoid their influences for forest bird species was 50 m and accordingly, FRAGSTATS calculated the core area of each forest patch. In addition, total patch size (ha), patch perimeter (m) and distance to nearest forest were also calculated.

### Landscape variables

The landscape around each focal patch was quantified in 2 × 2 squares km, so that each the bird point count was located in the centre of the square. This spatial scale has been previously used to study associations between passerine birds and landscape variables (e.g.

McGarigal and McComb 1995, Jokimäki and Huhta 1996, Villard et al. 1999). The IDRISI images were analysed with FRAGSTATS software (McGarigal and Marks 1995) to obtain landscape composition and configuration metrics.

Landscape composition, understood as the spatially non-explicit characteristics associated with the presence and amount of different patch types within a landscape (McGarigal and Marks 1995), was assessed by calculating the percentage of six widespread habitat types: burnt short shrublands, burnt tall shrublands, burnt shrublands with isolated pines, Aleppo pine forests, farmland and urbanised areas. The first three habitat types formed the burnt habitat matrix in which forest patches were embedded.

Landscape configuration refers to the physical distribution or spatial character of patches within the landscape (McGarigal and Marks 1995). Due to our interest in bird species associated with forests, we assessed only landscape configuration variables for forests. We selected variables that were known to influence animal distribution (McGarigal and Marks 1995): patch density, edge density, percentage of core forest area in the landscape, mean nearest-neighbour distance between forest patches and nearest-neighbour coefficient of variation. Patch density and edge density were calculated respectively as the number of forest patches and length of forest edges in 100 ha. Forest core area was defined analogously to the patch analysis, that is, as the percentage of forest within the buffer width of 50 m from forest edges, but for the total forest area in each of the 4 km<sup>2</sup> landscapes.

### Data analyses

The original number of local habitat, whole patch and landscape variables were separately grouped into a few independent factors using of principal component analysis (PCA) with a varimax normalised rotation. This procedure was established to reduce multicollinearity in the multivariate analysis of bird responses to habitat and landscape characteristics (Hinsley et al. 1995, Jokimäki and Huhta 1996, Díaz et al. 1998). The construction of three PCAs emphasises the multi-scale approach: the first analysis for local habitat (local scale), the second for patch (forest patch scale) and the third for 4 km<sup>2</sup>-landscape metrics (landscape scale). Structure and floristics were included in the same PCA because we considered that birds are influenced by them simultaneously. For the same reason, composition and configuration variables were included simultaneously in the PCAs performed for 4 km<sup>2</sup>-landscape metrics.

In order to assess the effects of landscape variables at increasing spatial scales, a backward step-wise multiple regression (Crawley 1993) using a hierarchical approach

Table 2. Variables describing the habitat structure and factor loadings of each variable in relation to the five first factors obtained in the principal component analysis (factor rotation: varimax normalised).

| Variable   | Quershrub | Amax    | Pinedens | Lowshurb | Tall tree |
|--|-----------|---------|----------|----------|-----------|
| Number of mature pines 100 m <sup>-2</sup>             | -0.16     | 0.12    | 0.86***  | -0.13    | 0.00      |
| Maximum vegetation height                              | 0.27      | 0.76*** | -0.15    | 0.15     | 0.28      |
| Cover of bare ground                                   | -0.09     | -0.07   | -0.19    | -0.09    | -0.04     |
| Cover of shrubs and grasses <25 cm tall (%)            | -0.17     | -0.06   | -0.19    | 0.05     | 0.10      |
| Cover of shrubs and grasses from 25 to 50 cm tall (%)  | 0.02      | -0.05   | -0.06    | 0.94***  | 0.12      |
| Cover of shrubs and grasses from 50 cm to 1 m tall (%) | 0.77***   | -0.11   | 0.25     | 0.22     | 0.20      |
| Cover of shrubs grasses from 1 to 2 m tall (%)         | 0.89***   | 0.12    | 0.08     | -0.06    | 0.23      |
| Cover of shrubs and trees from 2 to 4 m tall (%)       | 0.77***   | -0.01   | 0.11     | 0.00     | 0.24      |
| Cover of trees from 4 to 8 m tall (%)                  | 0.39*     | 0.04    | 0.79***  | 0.06     | 0.10      |
| Cover of trees from 8 to 16 m tall (%)                 | -0.04     | 0.88*** | 0.26     | -0.17    | -0.01     |
| Cover of trees > 16 m tall (%)                         | 0.24      | 0.13    | 0.06     | 0.12     | 0.93***   |
| Grasses  | -0.42*    | 0.19    | -0.20    | 0.12     | -0.17     |
| Species from Rosmarino-Ericion                         | -0.16     | -0.18   | 0.12     | 0.02     | -0.06     |
| Species from Oleo-Ceratonion                           | 0.25      | 0.10    | 0.04     | 0.34*    | -0.09     |
| Species from Quercion ilicis                           | 0.90***   | 0.14    | -0.16    | 0.02     | -0.11     |
| Eigenvalues  | 4.40      | 2.50    | 1.86     | 1.50     | 1.08      |
| % Variation explained                                  | 29.4      | 16.7    | 12.3     | 10.0     | 7.2       |

\*\*\*  $p < 0.001$ , \*\*  $p < 0.01$ , \*  $p < 0.05$ .

was employed (Buckland and Elston 1993). We conducted three different steps, using at each step the residuals obtained from the best model of the former step. In the first step, the number of species was taken as a dependent variable and local habitat factors as predictors. In the second step, we used the residuals of the former analysis as dependent variable and patch factors as predictors. Finally, in the third step, the residuals of the second regression and landscape factors were used as dependent variables and predictors, respectively. The step in which each set of variables was entered into the model was based on a hierarchical approach considering nested spatial scales at different steps. The analyses were performed separately for the number of canopy, understory and ubiquitous species. All statistical analyses were run with Statistica Statsoft 1999.

## Results

### Habitat and landscape PCAs

The principal component analysis conducted with local habitat variables (structure and floristics) gave five main factors, which accounted for 75.6% of the variance contained in the original data set. The first factor obtained in this PCA (Quershrub) represented at the same time a gradient of shrub structure and abundance of Quercion ilicis plants; the second (Amax), a gradient of vertical tree development; the third (Pinedens), a gradient of tree density; the fourth (Lowshrub), a gradient of cover of plants from 25 to 50 cm; finally, the fifth (Talltree) segregated the few point counts with very tall trees (Table 2).

Three factors, which accounted for 99.3% of total data matrix variance, were obtained from the PCA

performed with the variables that described the characteristics of the forest fragments where the bird census point counts were situated (Table 3). The first factor (Fragsize) represented forest size and total core area, the second factor (Fragisolat) was a gradient of fragment isolation and the third factor (Fragshape) determined a gradient from regular to irregular fragment shapes, that is to say, from low perimeter<sup>2</sup>/size rates to high ones.

The first five component loadings for 4-km<sup>2</sup> landscape composition and configuration variables accounted for 85.3% of the variance contained in the original data set (Table 4). The first factor in this PCA (Edgeland) represented a gradient of forest edges in the landscape, which were also positively related to the cover of urbanised areas, and negatively to the cover of low shrublands. The second factor (Pineland) represented a gradient from landscapes dominated by large pine forest tracts to landscapes with many forest patches but low total forest cover. The third (Farm-

Table 3. Variables describing the composition and configuration of the pine forest patch where the bird point count was located. Factor loadings of each individual variable in the first three factors obtained in the principal component analysis (factor rotation: varimax normalised) are also shown.

| Variable                | Fragsize | Fragisolat | Fragshape |
|-------------------------|----------|------------|-----------|
| Forest size             | 0.97***  | 0.12       | 0.19      |
| Forest perimeter        | 0.82***  | 0.12       | 0.54**    |
| Shape index             | 0.21     | 0.13       | 0.97***   |
| Core area               | 0.98***  | 0.11       | 0.11      |
| Near neighbour distance | -0.13    | -0.98***   | -0.13     |
| Eigenvalues             | 3.31     | 0.92       | 0.73      |
| % Variation explained   | 66.2     | 18.5       | 14.6      |

\*\*\*  $p < 0.001$ , \*\*  $p < 0.01$ , \*  $p < 0.05$ .

Table 4. Variables describing landscape composition and configuration in the landscape surrounding the bird point counts (4 km<sup>2</sup>). Factor loadings of each individual variable in the first five factors obtained in the principal component analysis (factor rotation: varimax normalised) are also shown.

| Variable  | Edgeland | Pineland | Farmland | Tallshrubland | Isolpineland |
|---|----------|----------|----------|---------------|--------------|
| Burnt short shrublands in 4 km <sup>2</sup>               | -0.72*** | 0.57**   | -0.12    | 0.16          | -0.25        |
| Aleppo pine forests in 4 km <sup>2</sup>                  | 0.62**   | -0.73*** | 0.07     | 0.12          | 0.08         |
| Burnt shrublands with isolated pines in 4 km <sup>2</sup> | 0.20     | 0.05     | -0.21    | 0.06          | 0.91***      |
| Burnt tall shrublands in 4 km <sup>2</sup>                | 0.03     | 0.21     | -0.09    | 0.95***       | -0.05        |
| Farmland in 4 km <sup>2</sup>                             | 0.16     | -0.02    | 0.91***  | 0.11          | -0.21        |
| Urbanised areas in 4 km <sup>2</sup>                      | 0.74***  | 0.03     | -0.38    | 0.25          | -0.36        |
| Patch density   | 0.30     | 0.89***  | 0.03     | 0.02          | 0.03         |
| Edge density  | 0.83***  | 0.10     | 0.07     | 0.01          | 0.22         |
| Forest core area in the landscape                         | 0.53*    | -0.78*** | 0.06     | 0.13          | 0.05         |
| Mean of near neighbour distance                           | -0.71*** | 0.02     | -0.21    | 0.10          | -0.10        |
| Coefficient of variation of near neighbour distance       | 0.04     | 0.80***  | 0.00     | -0.26         | 0.13         |
| Eigenvalues   | 4.02     | 2.25     | 1.25     | 0.99          | 0.86         |
| % Variation explained                                     | 36.6     | 20.5     | 11.4     | 9.0           | 7.8          |

\*\*\*  $p < 0.001$ , \*\*  $p < 0.01$ , \*  $p < 0.05$ .

land) and fourth factors (Tallshrubland) determined the cover of farmland and the cover of tall shrublands, respectively. Finally, the fifth factor (Isolpineland) determined the abundance of shrublands with isolated pines.

### Bird species and their associations with habitat and landscape factors

A total of 36 breeding bird species were recorded during the fieldwork (Table 1). The average number of bird species per point count was 12.3 (SD = 3.7), while the minimum and maximum values detected were 1 and 18 species, respectively. Of these 36 species, 18 were forest species (50%) (10 canopy species and 8 understorey species) and 18 (50%) ubiquitous species.

Canopy species were less affected by local habitat (22.5% of total variance explained by these factors) than by patch and landscape (35.4% of total variance explained by these factors) (Table 5). Within the local habitat variables, canopy species were only positively related to the vertical tree development (Amax). Once this local habitat factor was controlled for by using the residuals of the former regression model, fragment characteristics, which accounted for 29.1% of total variance, were the most important predictors for canopy species occurrence. Fragment size, core area and fragment perimeter (Fragsize) (6.3% of total variance) were positively associated with canopy species. But, more interestingly, forest shape (Fragshape) accounted for 22.8% of total variance, irregular shapes being positively associated with these species. After controlling for the smaller scales, the fourth factor of the PCA (Tallshrubland) was the only that entered into the model and the relationship between the cover of tall shrublands and the number of canopy species was positive.

In contrast with canopy species, species of the understorey were more affected by local habitat factors than by patch features (47.3% vs 12.1% of total variance, respectively) (Table 5). Understorey species were highly related to local habitat characteristics, specifically with the cover of shrubs from 0.5 to 4 m tall and the abundance of *Quercion ilicis* plants (Quershrub). Fragment characteristics were included in the model, but the overall percentage of explained variation was almost three times lower than in canopy species. As the canopy species, the understorey species were also positively affected by fragment size (Fragsize) and by fragment shape (Fragshape), although only marginally for this latter factor. At a landscape scale, no factor entered into the model after controlling for the effect of smaller scales.

The best model performed with ubiquitous species only accounted for 12.2% of total variance (Table 5). Only local habitat entered into the model of these species, which were negatively related to the presence of shrubs and *Quercion ilicis* plants (Quershrub).

## Discussion

### Importance of local habitat factors

Our results showed that local habitat features affected bird occurrence in all groups justifying the assumption that these group of variables are critical in predicting distribution of forest birds during breeding (Wiens 1989) and the need to be accounted for in landscape ecological studies. Tree vertical development was positively related to canopy species, whereas variation in pine density did not affect them. A similar relationship was found in Aleppo pine forest fragments surrounded by a farmland matrix, where forest species as a whole were positively associated with tall trees (Brotons and Herrando 2001). In Aleppo pine forests of SE Spain,

López and Moro (1997) showed that, while tall trees favoured forest species, pine density was not positively associated with any of these species. Therefore, as suggested by our studies and by these authors, management practices to reduce tree densities and favour tall pines would benefit forest species. It is especially interesting reporting that, in dry Aleppo pine forests, the selective thinning and pruning can simultaneously contribute to reduce pine density and increase the mean height of trees (Pastor-López 1995).

Understorey species were highly associated with the cover of shrubs and plants associated with holm-oak forests. López and Moro (1997) also found that holm-oaks and associated plant species appeared to be the main determinant of bird community composition and species richness in Aleppo pine forests. In our study area, the presence of holm-oaks implied mixed forests, with pines protruding from these oaks. This probably favoured also canopy birds, such as *Parus major*, *Parus caeruleus* or *Aegithalos caudatus*, that in the Iberian Peninsula prefer these broad-leaved trees, but did not decrease opportunities for those which prefer coniferous, such as *Parus cristatus* or *Certhia brachydactyla* (Tellería and Santos 1995). Moreover, greater arthropod availability in these oaks compared with Mediterranean pines (Illera and Atienza 1995) may

greatly enhance the populations of these broad-leaved tree dependent species, which implies an overall increase in forest bird species per point count. However, although the cover of shrubs and plants associated with the holm-oak exerted a positive effect on understorey species, it had a negative effect on ubiquitous species, within which there are no foliage-dwelling species that regularly use food sources located in trees (Perrins 1998). Therefore, the elimination of the understorey would influence negatively understorey species but positively ubiquitous species. Nevertheless, considering that the percentage of variation explained by these plants is higher in the model performed for understorey species than in that for ubiquitous species, hypothetical management practices in this direction would probably result more negative for understorey species than positive for ubiquitous.

### Relevance patch and landscape factors

Patch and landscape characteristics played a determinant role in breeding forest species occurrence in forests which configuration was highly affected by wildfires. Several studies carried out in fragmented temperate regions have also reported that this type of variables

Table 5. Hierarchic multiple regression models on bird species richness in forest patches. The models were conducted in three steps. Step 1: number of canopy species as dependent variable and local habitat factors as predictors; step 2: the residuals of the former analysis as dependent variable and fragment factors as predictors; step 3: the residuals from step 2 as dependent variables and landscape factors as predictors. At each step, a backward stepwise (p-to-enter = 0.05, p-to-remove = 0.10, n = 36 point counts) was used. Explained variation at each step was calculated with respect to the initial dependent variable (species group), not for the residuals. Results are given for canopy, understorey and ubiquitous species.

|                            | Coefficient | F     | p      | Explained variation |
|----------------------------|-------------|-------|--------|---------------------|
| <b>Canopy species</b>      |             |       |        |                     |
| Step 1: Local habitat      |             |       |        |                     |
| Amax                       | 1.03        | 9.88  | <0.01  | 22.5%               |
| Step 2: Fragment           |             |       |        |                     |
| Fragsize                   | 0.54        | 4.25  | <0.05  | 6.3%                |
| Fragshape                  | 1.04        | 15.54 | <0.001 | 22.8%               |
| Step 3: Landscape          |             |       |        |                     |
| Tallshrubland              | 0.53        | 4.62  | <0.05  | 6.3%                |
| Model                      |             |       |        | 57.9%               |
| <b>Understorey species</b> |             |       |        |                     |
| Step 1: Local habitat      |             |       |        |                     |
| Quershrub                  | 1.14        | 30.57 | <0.001 | 47.3%               |
| Step 2: Fragment           |             |       |        |                     |
| Fragsize                   | 0.52        | 8.28  | <0.01  | 8.8%                |
| Fragshape                  | 0.31        | 3.05  | <0.1   | 3.3%                |
| Step 3: Landscape          |             |       |        |                     |
| None                       |             |       |        |                     |
| Model                      |             |       |        | 59.4%               |
| <b>Ubiquitous species</b>  |             |       |        |                     |
| Step 1: Local habitat      |             |       |        |                     |
| Quershrub                  | -0.99       | 4.75  | <0.05  | 12.2%               |
| Step 2: Fragment           |             |       |        |                     |
| None                       |             |       |        |                     |
| Step 3: Landscape          |             |       |        |                     |
| None                       |             |       |        |                     |
| Model                      |             |       |        | 12.2%               |



accounted for a significant proportion of the total variance in forest bird occurrence, ranging from 20 to 50% (e.g. Pearson 1993, Jokimäki and Huhta 1996, Drapeau et al. 2000, Pino et al. 2000). Therefore, although some of these studies show significant landscape effects that might be in fact due to correlations between these and local habitat characteristics, on the whole, these results suggest that models of bird occupancy solely based on habitat characteristics could be misleading in fragmented landscapes.

Studies on the effect of fragmentation on birds have usually found a positive relationship between fragment size and the number of forest bird species (e.g. Bellamy et al. 1996, Tellería and Santos 1997, Díaz et al. 1998), which denotes the importance of habitat loss in structuring bird communities in fragmented woodlands. Similarly, we found a significant role of patch size in forest species, the larger forest fragments being those that were associated with higher number of species in point counts. The fact that, in our study case, bird richness in equal-sized bird point counts was dependent on size can be associated with two non-exclusive possible explanations. On one hand, very small forest patches may have not met minimum area required for some forest species and, therefore, these species may be absent from the point-counts located within those patches. On the other hand, the independence between size and other analysed variables such as isolation and forest shape also suggests that the habitat diversity hypothesis in relation to forest size (Berg 1997) may be an alternative explanation behind the positive relation between bird richness and patch size. Furthermore, the relationship between point forest bird richness and the size and configuration of forest patches indicates that bird assemblages in our forest mosaics did not fit the random sample hypothesis (Connor and McCoy 1979).

A spatial consequence of habitat fragmentation is the isolation of remnant patches of habitat. This study did not show any effect of isolation on species presence, which contrasts with two other studies carried out in Iberian pine forests patches, in which isolation played a significant role in bird assemblages (Díaz et al. 1998, Brotons and Herrando 2001). The importance of isolation differed in these two studies, since its effect was higher in the first (where the forest patches were surrounded by cereal croplands) than in the second (where the forest patches were surrounded by vineyards). In our case, we did not find effects of isolation in landscapes where the matrix was essentially a mosaic of burnt shrublands, thus suggesting that the forest fragmentation provoked by fires does not seem to isolate bird populations. All these results seem to indicate that the matrix type could be involved in the isolation of the forest fragments and thus in the composition of their bird assemblages (Mönkkönen and Reunanen 1999). However, in another study carried out in Iberian oak forest patches surrounded by cereal crops, Tellería and

Santos (1999) found a lack of effect of isolation on bird species occurrence. Therefore, even on a regional scale (e.g. the Mediterranean Iberian Peninsula), current knowledge is not sufficient to generalise about the role of isolation, thereby highlighting the relevance of the landscape context in predicting the effects of fragmentation on wildlife.

We found that forest species richness was highly favoured by irregular forest shapes (high perimeter<sup>2</sup>/size rates). This result suggests some positive effects of the length of edges for Mediterranean forest birds. However, forest edges have been commonly presumed to have deleterious biotic and abiotic consequences for the organisms that inhabit forest fragments (Murcia 1995). Within the negative biotic impacts, nest predation and brood parasitism may affect forest birds and, in highly fragmented forests, these impacts could be so high that nesting birds cannot fledge young enough to maintain stable populations (Donovan et al. 1995). In England, Hinsley et al. (1999) reported that the breeding performance of *Parus major* and *Parus caeruleus* declined as fragmentation increased. With regards to abiotic edge effects, Dolby and Grubb (1999) showed that strong winds and low temperatures affected negatively bird populations inhabiting highly fragmented temperate woodlands. In spite of the data suggesting negative edge effects for birds, Friesen et al. (1999) found that the distance from nests to the nearest forest edge did not significantly affect the nesting success of several Canadian forest bird species. Furthermore, Santos and Tellería (1992) found that Mediterranean forest patches differ from the usual pattern of nest predation found in other fragmented landscapes. These authors studied edge effects on predation of artificial avian nest in a forest archipelago situated in an agricultural area of central Spain and found a trend towards lower predation on the forest edge than in the interior. Moreover, Tellería and Santos (1992) reported for the same trail, a tendency of predation to increase as forest size class decreased. Therefore, in the Iberian Peninsula, available data suggest that forest edges do not lead to an increase in nest predation but small forests do. Our results are consistent with this suggestion since, on the one hand, fragment size was positively related to the richness of forest species and, on the other, high perimeter<sup>2</sup>/size rates positively influenced forest bird occurrence. Understorey species were less strongly related to forest shape than canopy species probably because birds that inhabit the shrubby understorey do not perceive edges between shrubby pine forests and shrublands as canopy species do.

Indeed, food availability may be another important factor behind positive boundary effects. Edges may have higher arthropod availability than forest interior (Jokimäki et al. 1998), which represents a positive edge factor for most forest birds with regard to the main food supply during the breeding season. Furthermore,

Forman (1995) showed that curvilinear boundaries and amoeboid shapes, such as those typically provoked by forest fires (see Chuvieco 1999 for data about the complex forms provoked by fire in eastern Spain), facilitated animal movements towards the immediate surroundings and provided new microenvironments. This author also suggested that this permeability may also be enhanced by low edge contrast in forest-shrubland boundaries compared with those of forest-farm-land or forest-urbanised areas. Therefore, although edges are often considered as negative for forest birds, our results support the rejection of such generalisations and show positive edge effects in particular landscapes.

In summary, our initial hypothesis that, apart from habitat loss, fire-related landscape change has a low impact in Mediterranean forest species can be confirmed since no negative effect was detected for isolation, and positive perimeter/size effects were observed for these species. As suggested by Telleria and Santos (1999), this seems to indicate that Mediterranean forests have been historically so heavily affected by fragmentation that interior forest birds are now very scarce or extinct and remaining species are well adapted to these heterogeneous landscapes (see also Mönk-könen and Welsh 1994 for similar processes in boreal forest mosaics).

Our analyses also showed that the contribution of patch and landscape differed depending on the ecology of each group studied. Within forest birds, understorey species were much less influenced by fragment and 4 km<sup>2</sup>-landscape characteristics than by local habitat, whereas the relationship was opposite for canopy species. This difference suggests that the fragmentation associated with fire regime may affect more strongly canopy than understorey species. For this last group, the resulting shrubby matrix does not differ much from their preferred habitat type, and hence, probably perceive a much less fragmented landscape than canopy species do.

The model for ubiquitous species, which had much less predictive power than those of forest species, did not include any patch feature. This could be related to the fact that this group of species is ecologically more diverse than the other two groups (forest canopy and forest understorey species), which implies that shared ecological patterns may be difficult to find. Nevertheless, our results contrast with other studies carried out in farmlands or landscapes subjected to timber exploitation, which showed that this group of species, sometimes called edge species, was related to fragmentation variables, especially to forest edges (Jokimäki and Huhta 1996, Bellamy et al. 1996). Hence, it is possible that, in the burnt areas, ubiquitous species do not respond to such variables as they do in other fragmented landscapes. Most of the variables concerned in our analyses seem to be marginal for this group, and probably other unanalysed landscape features may have

a greater relevance. In this context, Forman (1995) reported that ubiquitous species usually tend to concentrate in abrupt edges, such as those between grasslands and forests. Sisk et al. (1997) found in Mediterranean patchy woodlands of California that the occurrence and abundance of ubiquitous bird species were higher in forest fragments surrounded by grassland in those surrounded by shrubland. Hence, we suggest that the soft edge between the shrubby matrix and the remaining forest patches does not provide a suitable habitat for most of these species.

We found few landscape effects after controlling for the effect of smaller spatial scales. Probably the most relevant result was that the cover of forest in the landscape was not relevant for any group of birds, which is consistent with the absence of any effect of patch isolation. Therefore, these results suggest that the shrubby matrix is highly permeable for birds.

The only landscape variable that affected birds was the cover of tall shrublands in the 4-km<sup>2</sup> landscape, and only for the group of canopy species. It is quite surprising that these birds were not affected by the proportion of forests in the landscape but were positively affected by that of tall shrublands. The previously mentioned lack of associations between all forest species and patch isolation suggests that tall shrublands do not favour canopy species by enhancing landscape connectivity but rather by increasing habitat quality in forests surrounded by this type of vegetation. Hence, we believe that canopy species, which are clearly benefited from high perimeter<sup>2</sup>/size rates and thus seem more attracted than repelled by edges, may go to these adjacent habitats, which can be used as feeding sites by several of these species (Perrins 1998, unpubl.). The observation of stable breeding territories of canopy species in very isolated and small forests (we have recorded the breeding of *Certhia brachydactyla* and *Parus major* in forests as small as 0.4 ha) can only be explained by the use of adjacent tall shrublands (habitat supplementation, sensu Dunning et al. 1992). In contrast, understorey species, which in a local scale were highly related to the cover of shrubs, were not related to the cover of tall shrublands in the landscape. This may be also due to an enlargement of niche breadth in this group of birds. However, in this case, understorey species probably use not only tall shrublands but also short shrublands with or without isolated pines. Here, specific relationships between landscape characteristics and occurrence of understorey species may be difficult to reveal due to similar preference of other habitats supplementary to forests.

### Conservation implications

The main contribution of this study consists of showing the specific bird-landscape patterns in relation to

wildfires in the Mediterranean area. Because the present study is one of the first that deals with this kind of landscape, more studies will be welcomed to further expand our main results. We also believe that the data obtained may represent an appreciable contribution to landscape management. This is especially relevant because the importation of management guidelines across regions with different perturbation regimes and histories can be misleading (Forman 1995). Several conclusions may be drawn from a conservational perspective. First, although fires reduce the cover of available habitat for Mediterranean forest bird species, they simultaneously create new landscapes where the remaining forest patches are suitable habitats for these species. Second, forest management is not necessarily negative for birds. The concomitant increase of tree height derived from decreasing pine density by selective logging could even benefit forest canopy species, although the maintenance of forest shrubs is essential for understory species. Third, bearing in mind the fundamental role of patch features for the forest avifauna of these landscapes, actions that consider exclusively local habitat management can be insufficient or inappropriate. As also reported in other fragmented landscapes, patch size plays also a key role for promoting forest birds communities in Mediterranean landscapes. However, patch isolation did not affect bird occurrence and, irregular forest shapes with shrub-forest edge favoured the maintenance of a diverse forest bird community. Suggestions for spatial arrangement of forest patches, traditionally based on minimising perimeter/area rate, should be revised for Mediterranean forested landscapes affected by fires.

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