Research article

Bird assemblages in forest fragments within Mediterranean mosaics created by wild fires

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Abstract

The role of habitat heterogeneity as a key factor in determining species pools in habitat mosaics has been acknowledged, but we still know little on the relative importance of the different ecological processes acting within such complex landscapes. We compared species richness and distribution in forest fragments imbedded in shrublands to those in continuous forests or in continuous shrublands. We examined the consistency of our data with the predictions of two hypotheses: 1) the "*Habitat fragmentation hypothesis*" which states that fragmentation has negative effects on the species from the original continuous habitat; 2) the "*Habitat supplementation /complementation hypothesis*" which stipulates that the presence of a matrix habitat around the fragments will mitigate negative effects on the species from the original habitat (*supplementation*) or allow the presence of species that depend on the presence of both the fragment and matrix habitats (*complementation*). We show that: 1) species richness in forest fragments did not differ from species richness in segments of continuous forests of equal area; 2) the bird community of forest fragments got impoverished in some forest species but a higher proportion of species common in continuous forests were not affected by fragmentation; 3) fragment communities had a significant proportion of common species that were scarce in, or absent from both continuous forests and shrublands. While, a few forest species supported predictions from the fragmentation hypothesis, occurrence patterns observed in several other species were consistent with either the supplementation or the complementation hypotheses. Our results suggest that there is no single hypothesis that properly captures the consequences of a shift from continuous forests to a mosaic of forest fragments and shrublands and that different ecological mechanisms act in conjunction to determine species pools in habitat mosaics. Habitat heterogeneity at a local scale appears a key factor in maintaining bird diversity in fire driven Mediterranean landscapes.

Introduction

Recent large-scale changes in land use patterns have increased the need to understand how landscape structure affects species distribution (Forman 1995). In this context the fragmentation of once continuous ecosystems and of forests in particular, has gained a pre-eminent role in the study of animal responses to the spatial re-arrangement of the landscape (Saunders et al. 1991; Andrén 1994; Murcia 1995). Fragmentation has been defined as the transformation of "a large expanse of habitat (...) into a number of fragments of smaller total area (separated) from each other by a matrix of habitats unlike the original" (Saunders et al. 1991; Fahrig 2003). Derived from the equilibrium theory of island biogeography (MacArthur and Wil-

son 1967), studies on the effects of habitat fragmentation on species distribution often relied on a "fragment centred" approach (Wiens 1994; Haila 2002), often perceiving fragments as isolates within a hostile matrix. The development of metapopulation theory has reinforced this tradition (Hanski and Gilpin 1991), which, until recently, mostly ignored the interactions among the different elements coexisting in real landscapes. Despite this, these studies often dealt with processes that implicitly assumed ecological interactions between different elements of the landscape (i.e., increased nest predation in fragments due to predators from neighbouring areas, Paton 1994; Murcia 1995). Other studies, however, were explicitly interested in how the matrix affected the communities of habitat fragments (Santos and Tellería 1992; Wiens 1994; Sisk et al. 1997; Mönkkönen and Reunanen 1999) and often showed the inadequacy of viewing them as islands (Norton et al. 2000; Brotons et al 2003). Finally, recent reviews of the results of mensurative or experimental studies on habitat fragmentation (Debinski and Holt 2000; McGarigal and Cushman 2002) suggested that concepts from island biogeography and metapopulation theory were inappropriate for many analyses of habitat fragmentation. They concluded that the effects of fragmentation were (1) multicausal, (2) heavily influenced by the amount of structural differences between matrix and fragments (see Brotons et al. 2003); (3) dependent on the temporal and spatial scales of observation and on system history (Bissonette and Storch 2002).

The Mediterranean region provides good examples of complex and dynamic landscapes. There, human intervention has shaped a mosaic of agriculture, scrub and forest patches (Blondel and Aronson 1999). Wild fires are part of that history (Trabaud 1981; Moreira et al. 2001). They have created mosaics with forest patches embedded in a matrix dominated by shrublands and an overall rarity of large forest tracts. Ecological consequences of habitat fragmentation and landscape heterogeneity in Mediterranean mosaics have been little studied (Rocamora 1997; Preiss et al. 1997) and have focused on forest fragments in a matrix of agriculture (Tellería and Santos 1995; Shochat et al. 1001; Santos et al. 2002). Studies to date suggested a lower impact of fragmentation per se on forest birds in the Mediterranean (Herrando and Brotons 2002; Santos et al. 2002) than in central and northern Europe (Saunders 1981; but see Schmiegelow and Mönkkönen 2002). Santos et al. (2002) argued that this could result from the elimination of the forest species most sensitive to fragmentation because of the long history of habitat perturbation in this region (see also Covas and Blondel 1998).

We studied the bird communities of forest fragments surrounded by a matrix of shrublands created by wild fires and compared them to communities of continuous forests and of continuous shrublands. We analysed the consistency of the patterns observed with predictions from two main hypotheses relevant to the distribution of birds in fragments of once continuous habitats. 1) The "*habitat fragmentation hypothesis*" (Saunders et al. 1991; Fahrig 2003), which is part of the genealogy of hypotheses stemming from the island biogeography approach (Haila 2002) and states that fragmentation had negative effects on the species from the original continuous habitat, negative effects related (i) to reduced area, (ii) to increased isolation between fragments and (iii) to changes in habitat structure near forest edges (Andrén 1994). These negative effects should increase with decreasing fragment size. 2) The "*habitat supplementation / complementation hypothesis*" (Dunning et al. 1992) which stems from a landscape centred approach. It stipulates that the presence of matrix habitats and their resources (i.e., food, habitat cover or nesting sites) will mitigate negative effects of fragmentation on species from the original habitat (supplementation) or that bird species found neither in the matrix nor in the continuous forest could be present and abundant in the mosaic of fragment and matrix habitat (complementation). The *Habitat complementation hypothesis* has been recently interpreted as a positive fragmentation effect (Fahrig 2003) because it predicts the probability of species occurrence to increase as the amount of the complementing matrix habitat increases (i.e., patch size of original habitat decreases). Therefore, since species requiring complementation of habitats will be rare or absent in large forest patches, this hypothesis predicts that species occurrence should increase with decreasing average fragment area (McCollin 1998).

Methods

Study area

Fieldwork was carried out in the Catalan coastal mountain range, south-west of the city of Barcelona (Northeast of the Iberian Peninsula, 41°36′ N, 1°16′ E, Figure 1). The study area ranged from 100 to 700
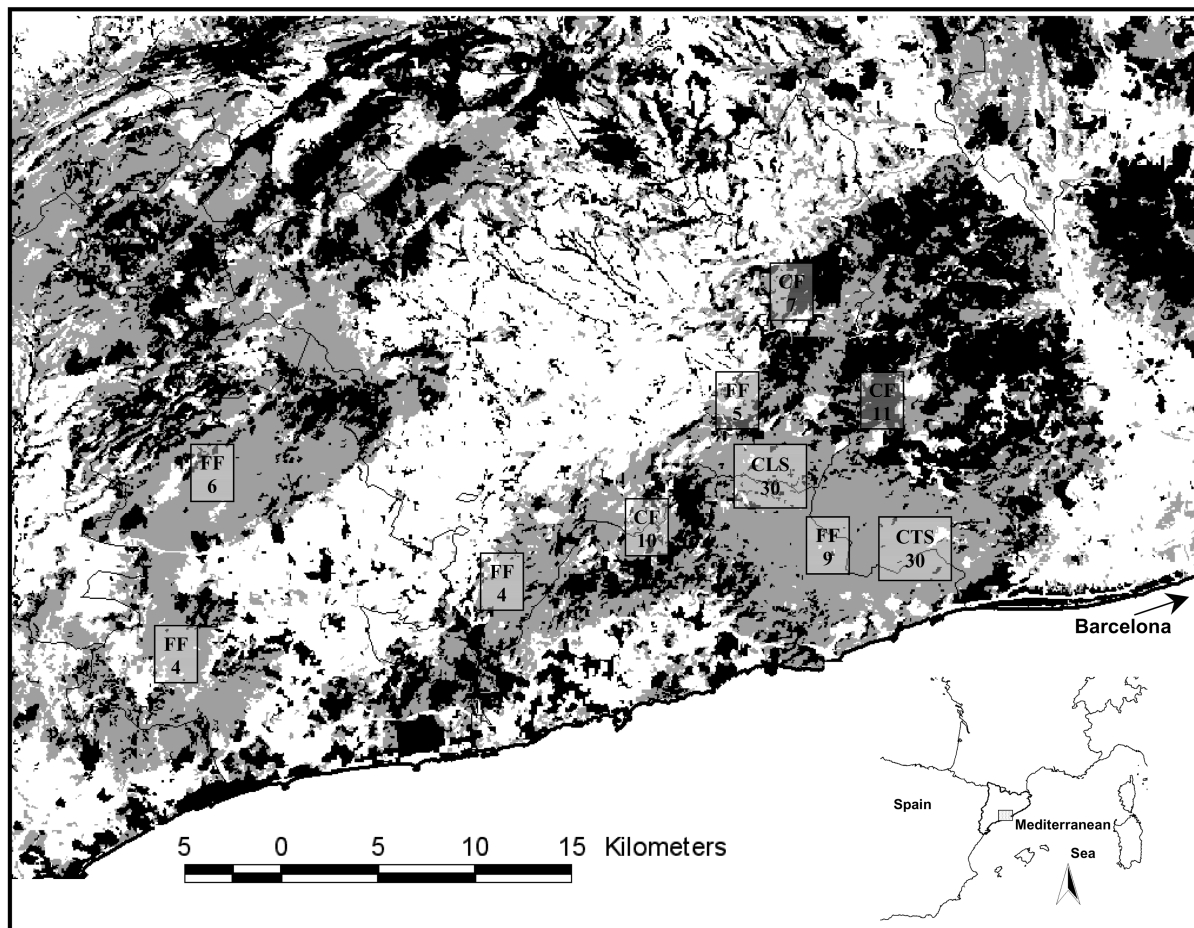
Figure 1. Geographic location and land use map of the study area based on a Landsat satellite image. Black zones represent forests, soft grey represent shrublands burnt in last decades, and white zones represent farmland and urbanised areas. Boxes show the approximate distribution of sampling sites in different habitats and their number grouped by geographic location. Continuous tall shrublands (CTS), continuous low shrublands (CLS), continuous forests (CF), forest fragments (FF). See methods for more details on distribution of sites within each habitat.

m a.s.l and was located between the mesic "meso-Mediterranean" and the xeric "thermo-Mediterranean" life zones (Folch 1986). Secondary low shrubby formations (*Rosmarino-Ericion*) and Aleppo pine (*Pinus halepensis*) forests dominated the landscape. These formations are prone to wild fires. In forest areas dominated by Aleppo pines, fires kill the trees and burn the above-ground parts of the shrubs. Because most of the shrub species re-sprout vigorously from their roots, the burned areas turn into a matrix of heterogeneous shrubland interspersed by forest fragments (Trabaud 1981; see Herrando and Brotons 2002 for more information on the study area). Vegetation within forest fragments created by fire may differ from undisturbed forests due to the burning of the ground vegetation, or to pre-existing

local habitat characteristics that made these areas less fire sensitive (i.e., smaller amounts of combustible fuel in terms of lower tree densities, Pausas 1998).

Study design

Using aerial photographs (1:25 000, Institut Cartografic de Catalunya 1997) we identified 1) areas with fragments of Aleppo pine forests surrounded by a matrix of shrubland, 2) areas of continuous forest, and 3) areas of continuous shrublands (Figure 1).

Forest fragments and their matrix − We selected 28 forest fragments larger than 1 ha. The area of each fragment was calculated from the photograph (mean area = 10.16 ha; SE = 11.9; range: 1 to 59 ha). Forest fragments were selected so that (1) at least 75%

of the matrix consisted of shrubland created by fires 3 to 18 years before the study, (2) there were at least 2 km between selected forest fragments. This minimum distance between fragments ensured that the area of matrix accessible to birds from a fragment did not overlap with the area of matrix accessible from another fragment. As song birds establish territories centred around their nests during the breeding season, this distance also ensured that different individuals were sampled in different fragments. In keeping with fragment selection criteria, we defined a 2 by 2 km square centred on each forest fragment in which we calculated the proportion of shrubland, of agriculture and of other land uses (Herrando and Brotons 2002). Farmland habitats, in particular, can provide highly valued food resources. Thus, we analyzed the proportion of farmland around the fragments.

Continuous forest − Within the region from which forest fragments had been selected, we chose three areas with continuous forests. Continuous forests had to be at least 300 ha in size and unaffected by wild fires for at least 50 years (Herrando et al. 2003).

Continuous shrubland − We selected two areas of homogenous continuous shrubland (> 1000 ha each). The first consisted of low shrubs and open areas (continuous low shrublands) that resulted from a wild fire in 1994 to the east of the Catalan coastal mountain range (Garraf massif). The second was dominated by tall shrubs and low cover of immature pines (continuous tall shrublands) resulting from a wild fire in 1982 in the same area. Both represented typical stages of shrublands created by fire (Herrando et al. 2003) and we considered that they were representative of the shrublands found in the matrix surrounding the forest fragments.

Bird sampling

We placed 28 sampling sites in the forest fragments, 28 in the continuous forests, 30 in the continuous tall shrublands and 30 in the continuous low shrublands.

In continuous forests, continuous tall shrublands and continuous low shrublands sampling sites were distributed along access trails across the different study areas but at least 400 m apart to avoid double counts. They were located at more than 100 m from the forest edge. In forest fragments we had one sampling site per fragment. It was located between 50 and 100 m from the fragment edge.

Sites in continuous forests and continuous shrublands were sampled in the spring of 1997 and re-sampled in 1998 to test for year effects, except for 6 sites in continuous forests that were only sampled in 2000. Sites in forest fragments were sampled in 2000.

We used the point-count method (Bibby et al. 1992) to sample birds. We visited each point-count site twice during the breeding season in March-April and in May-July. At each visit the observer recorded the species seen or heard during 10 minutes within a 100-m radius (Drapeau et al. 1999). The point-count sampling took only place during the 3 hours after dawn (peak of bird activity), and only in the absence of rain or strong wind. We excluded raptors, owls and nightjars from the data because they are not reliably detected with this technique (Bibby et al. 1992), as well as birds only observed flying overhead. As we were interested in the actual use of the habitats studied by birds we retained only the species for which we had evidence that they used a given habitat for breeding (e.g., nest construction or feeding young), foraging, or singing (perches), or species that were detected on both visits (see Díaz et al. 1998). For seven fragment sites in which the forest edge was less than 100 m from the observer, birds observed within the 100 m radius but outside the forested area were excluded from the analysis. There was no bias, however, with respect to fragment size given that three of these sites were located in relatively large forest fragments (20-60 ha) and four in small forest fragments (< 4 ha).

Local habitat structure

As forest vegetation structure is a key factor explaining bird diversity (Robinson and Holmes 1984; López and Moro 1997), we sampled habitat structure at each sampling site within a 50-m radius around the observer. 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, 2–4m, 4–8m, 8–16 m, > 16m), the maximum height of the vegetation and the number of adult pine trees in 100 m^2. Within each vegetation layer, the relative cover was defined as the projection of the foliage volume of the layer on a horizontal plane. This was estimated by comparison with a reference% cover chart (Prodon and Lebreton, 1981).

Statistical analyses

To estimate variation in species composition between samples, we first calculated Jaccard's similarity index between pairs of individual point-count sites:

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

where a is the number of species shared by samples x_1 and x_2, b the number of species observed only in the sample x_1 and c the number observed only in the sample x_2 (Legendre and Legendre 1998). We then calculated for any one of our point-count sites the mean similarity indexes of the birds observed in this site with those in any other site, either within the same sampling category, or from another sampling category. We used paired ANOVA tests and post hoc comparisons (Newman-Keuls test) to compare the mean similarity indexes obtained within and between habitat comparisons.

We used correspondence analysis (CA) to further explore the differences in bird communities between habitat types. Correspondence Analysis is a descriptive and exploratory technique using multi-way tables to analyse correspondences between, for example, sampling sites and species (Greenacre 1984; Legendre and Legendre 1998). We only included the species detected in at least 5% of the sites or in at least 10% of the sites of a single habitat type to limit undesired effects caused by rare species (Greenacre 1984).

Differences in species occurrence between sample categories were also analysed by means of generalised linear models with binomial error (logistic regressions, Crawley 1993) using habitat (four categories) as an explanatory variable in the analysis. *A posteriori* differences between sampling categories were tested using parameter estimates from the different habitat categories (Crawley 1993). We used logistic regressions to analyse bird species occurrence in fragments in relation to fragment area, or to the proportion of agriculture in the matrix. We modelled the two latter variables by first accounting for any marginally significant ($P < 0.1$) effect of vegetation variables. The effect of vegetation structure was estimated using the first five principal components from a Principal Components Analysis (PCA, Legendre and Legendre 1998) describing the vegetation structure observed at the sampling sites. For each signifi-

cant association between bird species and fragment area or proportion of agricultural land in the surrounding landscape, we determined the sign of the relationship (positive or negative) and its statistical significance, using the change in model deviance when removing the variable considered. To assess the final amount of variance explained by the model, we used Nagelkerke R^2 (Nagelkerke 1991) a measure analogous to the coefficient of determination R^2 in linear regression. All statistical analyses were run with Statistica, Statsoft, Inc 1999, and Canoco softwares.

Results

The average number of species recorded per site did not vary across years ($F_{1,73} = 6.97$, $P = 0.11$, comparison of 1997 and 1998 censuses), for all the habitats analysed ($F_{2,73} = 1.28$, $P = 0.28$). Only four species (Great tit, *Parus major*, Turtle dove, *Streptotelia turtur*, Green woodpecker, *Picus viridis*, and Greenfinch, *Carduelis chloris*) showed a weak but significant year effect.

Species richness

A total of 45 bird species were recorded (Table 1). The number of species detected was highest in forests, with 35 species recorded in forests fragments and 29 in continuous forest. Twenty six species were recorded in continuous tall shrublands and 19 in continuous low shrublands.

There was no difference in average species richness per site between forest fragments and continuous forests (post-hoc Newman-Keuls test, $P = 0.89$, Figure 2; post-hoc Newman-Keuls test, $P = 0.46$ when only continuous forests sites censused in 2000 were considered) nor between tall and low shrublands (post-hoc Newman-Keuls test, $P = 0.65$, Figure 2). Average species richness per site was significantly lower in shrublands than in forests ($F_{3,112} = 72.39$, $P < 0.0001$, Figure 2).

Similarity analyses

The bird assemblages from sites in continuous forests were more similar to the ones from other sites in continuous forests than to those from forest fragments (value and S.D. of mean similarity index within continuous forests $= 0.43 \pm 0.05$, forest fragments-

Table 1. List of the bird species recorded and % of sites in which it was observed in each habitat category. The same letters between species identify non-significant differences in the % of observation; different letters identify significant differences in % of observation. Differences were estimated by logistic regression models.

Species common and scientific names (Acronym)		Continuous low shrubs (n=30)	Continuous high shrubs (n=30)	Continuous Forests (n=28)	Forest fragments (n=28)
Red-legged Partridge	*Alectoris rufa* (ALRU)	0.70 (a)	0.20 (b)	0.00 (b)	0.07 (b)
Wood Pigeon	*Columba palumbus* (COPA)	0.00 (a)	0.03 (a)	0.64 (b)	0.71 (b)
Turtle Dove	*Streptopelia turtur* (STTU)	0.00 (a)	0.03 (a)	0.36 (b)	0.39 (b)
Common Cuckoo	*Cuculus canorus* (CUCA)	0.00 (a)	0.10 (a)	0.36 (b)	0.46 (b)
Wryneck	*Jynx torquilla* (JYTO)	0.00 (a)	0.00 (a)	0.00 (a)	0.11 (b)
Green Woodpecker	*Picus viridis* (PIVI)	0.07 (a)	0.00 (a)	0.46 (b)	0.29 (b)
Thekla Lark	*Galerida theklae* (GATH)	0.17 (a)	0.07 (ab)	0.00 (b)	0.00 (b)
Woodlark	*Lulula arborea* (LUAR)	0.00 (a)	0.00 (a)	0.07 (a)	0.21 (b)
Tawny Pipit	*Anthus campestris* (ANCA)	0.23 (a)	0.03 (b)	0.00 (b)	0.00 (b)
Wren	*Troglodytes troglodytes* (TRTR)	0.00 (a)	0.17 (a)	0.96 (b)	0.54 (c)
Robin	*Erithacus rubecula* (ERRU)	0.00 (a)	0.00 (a)	0.29 (b)	0.21 (b)
Stonechat	*Saxicola torquata* (SATO)	0.50 (a)	0.43 (a)	0.00 (b)	0.00 (b)
Nightingale	*Luscinia megarhynchos* (LUME)	0.00 (a)	0.13 (a)	0.64 (b)	0.54 (b)
Black-eared Wheatear	*Oenanthe hispanica* OEHI)	0.87 (a)	0.20 (b)	0.00 (c)	0.00 (c)
Rock Thrush	*Monticola saxatilis* (MOSA)	0.07 (a)	0.03 (a)	0.00 (a)	0.00 (a)
Blackbird	*Turdus merula* (TUME)	0.17 (a)	0.57 (b)	0.96 (c)	0.93 (c)
Mistle thrush	*Turdus viscivorus* (TUVI)	0.00 (a)	0.00 (a)	0.00 (a)	0.04 (a)
Cetti's Warbler	*Cettia cetti* (CECE)	0.00 (a)	0.10 (a)	0.06 (a)	0.00 (a)
Melodious warbler	*Hippolais polyglotta* (HYPO)	0.00 (a)	0.00 (a)	0.07 (a)	0.07 (a)
Dartford Warbler	*Sylvia undata* (SYUN)	0.97 (a)	0.93 (a)	0.00 (b)	0.11 (b)
Subalpine warbler	*Sylvia cantillans* (SYCA)	0.00 (a)	0.00 (a)	0.04 (a)	0.00 (a)
Sardinian Warbler	*Sylvia melanocephala* (SYME)	0.67 (a)	0.93 (b)	1.00 (b)	1.00 (b)
Blackcap	*Sylvia atricapilla* (SYAT)	0.00 (a)	0.00 (a)	0.14 (a)	0.07 (a)
Chifchaf	*Phylloscopus collybita* (PHCO)	0.00 (a)	0.00 (a)	0.04 (a)	0.00 (a)
Bonelli's Warbler	*Phylloscopus bonelli* (PHBO)	0.00 (a)	0.00 (a)	0.64 (b)	0.46 (b)
Firecrest	*Regulus ignicapillus* (REIG)	0.00 (a)	0.07 (a)	0.61 (b)	0.18 (a)
Long-tailed Tit	*Aegithalos caudatus* (AECA)	0.00 (a)	0.07 (a)	0.61 (b)	0.32 (c)
Spotted flycatcher	*Muscicapa striata* (MUST)	0.00 (a)	0.00 (a)	0.00 (a)	0.21 (b)
Crested Tit	*Parus cristatus* (PACR)	0.00 (a)	0.00 (a)	0.75 (b)	0.68 (b)
Coal Tit	Parus ater *(PAAT)*	0.00 (a)	0.00 (a)	0.21(b)	0.07 (ab)
Blue Tit	*Parus caeruleus* (PACA)	0.00 (a)	0.00 (a)	0.07 (a)	0.14 (a)
Great Tit	*Parus major* (PAMA)	0.13 (a)	0.50 (b)	0.86 (c)	0.79 (c)
Golden Oriole	*Oriolus oriolus* (OROR)	0.00 (a)	0.03 (a)	0.18 (b)	0.50 (c)
Short-toed Treecreeper	*Certhia brachydactyla* (CEBR)	0.00 (a)	0.00 (a)	0.64 (b)	0.61 (b)
Southern Grey Shrike	*Lanius meridionalis* (LAME)	0.60 (a)	0.37 (a)	0.00 (b)	0.00 (b)
Woodchat Shrike	*Lanius senator* (LASE)	0.17 (ab)	0.00 (a)	0.00 (a)	0.25 (b)
Jay	*Garrulus glandarius* (GAGL)	0.00 (a)	0.03 (a)	0.54 (b)	0.32 (c)
Serin	*Serinus serinus* (SESE)	0.27 (a)	0.47 (a)	0.82 (b)	0.82 (b)
Greenfinch	*Carduelis chloris* (CACH)	0.10 (a)	0.07 (a)	0.29 (a)	0.50 (b)
Goldfinch	*Carduelis carduelis* (CACA)	0.03 (a)	0.03 (a)	0.11 (a)	0.46 (b)
Linnet	*Acanthis cannabina* (ACCA)	0.00 (a)	0.00 (a)	0.00 (a)	0.04 (a)
Rock Bunting	*Emberiza cia* (EMCI)	0.03 (a)	0.03 (a)	0.07 (a)	0.11 (a)
Cirl bunting	*Emberiza cirlus* (EMCR)	0.00 (a)	0.00 (a)	0.00 (a)	0.18 (b)
Ortolan Bunting	*Emberiza hortulana* (EMHO)	0.07 (a)	0.03 (a)	0.00 (a)	0.00 (a)
Corn Bunting	*Miliaria calandra* (MICA)	0.23 (a)	0.00 (b)	0.00 (b)	0.07 (ab)

continuous forests index = 0.35 ± 0.05, $F_{1,54}$ = 31.49, $P < 0.0001$). Bird assemblages varied as much within sites from forest fragments than between sites from fragments and continuous forests (within forest fragments mean similarity index = 0.37 ±

0.09, forest fragments-continuous forests = 0.35 ± 0.05, post hoc Newman Keuls test, $P = 0.12$).

Bird assemblages from forest fragment sites differed significantly from those observed in shrublands, both low and tall shrublands combined (mean
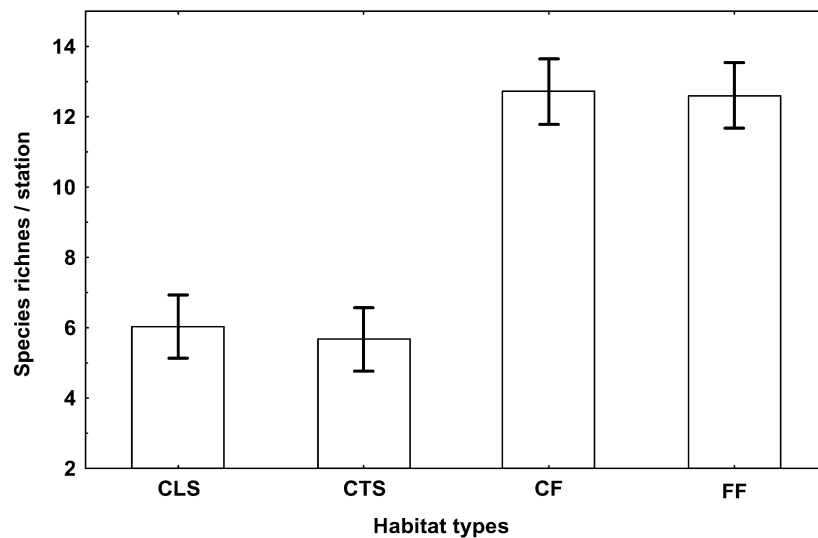
Figure 2. Representation of the mean number of species per site detected in each of the four habitat types analysed: continuous forests (CF), forest fragments (FF), continuous tall shrublands (CTS), continuous low shrublands (CLS).

similarity index $\pm$ S.D., within forest fragments = 0.37 $\pm$ 0.09, forest fragments-tall shrublands = 0.18 $\pm$ 0.05, post hoc Newman Keuls tests, $P < 0.0001$, forest fragments-low shrublands index = 0.09 $\pm$ 0.04, post hoc Newman Keuls tests, $P < 0.0001$).

Multivariate analyses

The two first axis of the Correspondence Analysis summarized 30% of the total variance (22% for the first axis, CA1 and 8% for the second, CA2). The first axis (CA1) opposed the shrubland sites and their associated bird species (positive scores, Figure 3) to those from the continuous and fragmented forests (negative scores, Figure 3) (post-hoc Newman-Keuls test, $P < 0.0001$, in all cases). Scores of sites from continuous forests and from forest fragments did not differ significantly along the first axis (post-hoc Newman-Keuls test, all data, $P = 0.36$, only continuous forests sites sampled in 2000, $P = 0.29$). Low shrublands sites ranked more positive along the first axis than those of tall shrublands (post-hoc Newman-Keuls test, $P < 0.001$). The second axis (CA2) significantly segregated the sites from forest fragments (positive scores, Figure 3) from those of continuous forests (negative scores) (Post-hoc Newman-Keuls test, all data, $P < 0.001$, only using continuous forests sites sampled in 2000, $P < 0.0001$).

Species specific patterns of occurrence

Nine of the 13 species observed in over 50% of the sites in continuous forests were observed with similar frequencies in forest fragments. The four remaining species had significantly lower frequencies in forest fragments: the Wren, the Firecrest, the Long-tailed tit and the Jay (Table 1). Eight species (the Wood-chat shrike, the Cirl bunting, the Spotted flycatcher, the Wryneck, the Golden oriole, the Goldfinch, the Greenfinch and the Woodlark) were more common in forest fragments than in continuous forests or in continuous shrublands (Table 1, Figure 3). Only three species, abundant in shrublands, were also occasionally observed in forest fragments, the Corn bunting, the Dartford warbler and the Red-legged partridge. One species, the Sardinian warbler, was common in all four sampling categories.

Species richness, species occurrence and fragment area

Habitat structure in sites from continuous forest and from forest fragments (Table 2) was similar, except for significantly less cover in shrubs of medium height and lower tree density in forest patches. Agricultural land in the matrix ranged between 0 and 18% (mean $\pm$ S.D., 5.3 $\pm$ 5.9) and we observed a positive relationship between the amount of cultivated land in the matrix and the occurrence of three species
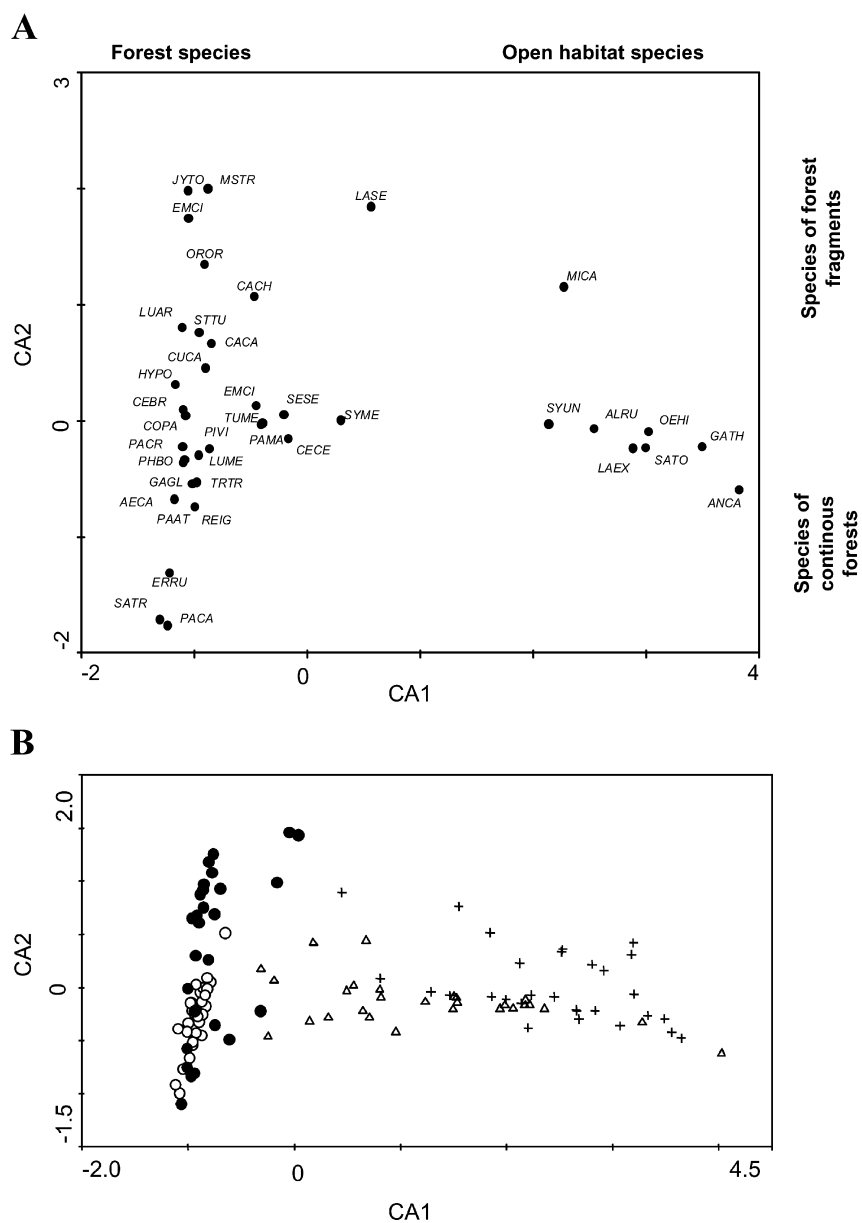
A

B

Figure 3. Ordination diagram showing the first two axes from a correspondence analysis (CA) of the bird species versus sites matrix. Text on the upper (first axis, CA1) and right side (second axis, CA2) of the diagram represents the extremes of the interpreted ecological gradients associated with each of the two CA axes. In (B), dots represent scores of forest fragments sites, open circles continuous forest sites, open triangles continuous tall shrublands sites and crosses continuous low shrublands sites.

(the Goldfinch, the Greenfinch and the Cirl bunting) (Table 4). After local habitat variables summarised by PCA (Table 3) had been taken into account, there was no significant correlation between species richness per site and fragment area (AREA, $F_{1,26}$ = 2.7, P = 0.15). However, the abundance of eight of the species recorded in forest fragments was positively correlated to fragment area (Table 4). Three of these species were significantly more frequent in continuous forests than in fragments (the Wren, the Firecrest and the Long-tailed tit); four of the remaining five species (the Crested tit, the Short-toed tree-creeper, the Jay and the Coal tit) were also more often observed in continuous forests than in fragments, but the differ-

Table 2. Mean values for habitat variables and their standard deviations (in parentheses) in the sites studied in the habitat categories. * = indicate significant differences (*P < 0.05*) in t-tests comparing continuous forests and forest fragments (after Bonferroni corrections).

Local habitat variables	Continuous low shrubs	Continuous tall shrubs	Continuous forests	Forest fragments
Maximum vegetation height (m)	1.60 (0.44)	2.80 (0.99)	14.79 (3.26)	13.29 (3.07)
Cover of bare ground (%)	22.33 (8.98)	9.63 (7.98)	4.61 (4.96)	6.54 (7.79)
Cover of shrubs and grasses less than 25 cm tall (%)	55.00 (14.32)	31.33 (16.76)	41.25 (25.00)	39.64 (17.10)
Cover of shrubs and grasses from 25 to 50 cm tall (%)	43.33 (10.93)	53.33 (17.09)	38.21 (15.65)	40.71 (14.89)
Cover of shrubs and grasses from 50 cm to 1 m tall (%)	8.77 (9.00)	49.17 (20.00)	42.14 (15.24)	29.11 (13.06)*
Cover of shrubs grasses from 1 m to 2 m tall (%)	1.77 (1.85)	15.93 (14.87)	26.61 (16.33)	15.46 (15.28)*
Cover of shrubs and trees from 2 m to 4 m tall (%)	0.07 (0.25)	2.53 (4.33)	14.32 (10.38)	13.57 (11.90)
Cover of trees from 4 m to 8 m tall (%)	0.00	0.07 (0.25)	29.46 (15.11)	25.75 (16.03)
Cover of trees from 8 m to 16 m tall (%)	0.00	0.00	26.07 (19.07)	21.61 (16.89)
Cover of trees more than 16 m tall (%)	0.00	0.00	3.64 (10.59)	0.07 (0.26)
Number of mature pines / 100 m^2	0.00	0.00	11.84 (8.51)	7.64 (4.96)*

Table 3. Habitat structure variables loadings on axis 1 to 5 of Principal Component Analysis . The five axis are ranked according to decreasing eigenvalue and summarise 78% of the variance in the data. Axis 1 = correlated with tall shrub cover (TALLSH); axis 2 = correlated with tree height (THEIGHT), axis 3 = correlated with bare cover (BGROUND), axis 4 = correlated with pine density (DENS), axis 5 = correlated with cover of low shrub (LOWSH).

Variable	TALLSH	THEIGHT	BGROUND	DENS	LOWSH
Number of mature pines / 100 m^2	− 0.07	− 0.11	0.21	0.79	0.32
Maximum vegetation height	− 0.03	0.91	0.08	− 0.05	− 0.01
Cover of bare ground	− 0.05	0.03	0.87	0.09	− 0.17
Cover of shrubs and grasses less than 25 cm tall (%)	− 0.18	− 0.02	0.21	− 0.68	0.32
Cover of shrubs and grasses from 25 to 50 cm tall (%)	− 0.01	− 0.02	− 0.07	0.02	0.88
Cover of shrubs and grasses from 50 cm to 1 m tall (%)	0.83	0.03	− 0.28	− 0.02	0.28
Cover of shrubs grasses from 1 m to 2 m tall (%)	0.90	0.21	0.04	0.09	− 0.17
Cover of shrubs and trees from 2 m to 4 m tall (%)	0.86	− 0.11	− 0.02	0.05	− 0.07
Cover of trees from 4 m to 8 m tall (%)	0.35	− 0.19	− 0.54	0.31	− 0.28
Cover of trees from 8 m to 16 m tall (%)	− 0.11	0.68	− 0.47	0.02	− 0.36
Cover of trees more than 16 m tall (%)	0.39	0.68	0.33	− 0.12	0.21
Eigenvalues	2.58	1.86	1.56	1.22	1.37
% Variation explained	0.23	0.17	0.14	0.11	0.12

ence was not significant. The abundance of three of the six species that were more often recorded in forest fragments was negatively affected by fragment area (decreasing occurrence with increasing fragment area; Spotted flycatcher, Wood chat shrike and Green finch). Fragment area was also negatively correlated with abundance in four additional species (the Turtle dove, the Corn bunting, the European cuckoo and the Wood lark, Table 4).

Discussion

Bird communities in Mediterranean forest fragments

The bird communities in forest fragments (35 species) were not impoverished in species when compared to continuous forests (29 species), but their species assemblage differed from that in continuous forests. Similarity index analysis and the correspondence analysis (Figure 3A) both indicated that bird assemblages in forest fragment sites were more heterogeneous than those in sites from continuous forests and that bird assemblages in shrubland sites were more heterogeneous (lower within habitat type mean similarity indexes) than those in forest sites.

The four species observed in continuous forests and in fragments, but that were significantly less abundant in fragments, had already been identified as species sensitive to forest fragmentation (Díaz et al. 1998; Brotons and Herrando 2000; Santos et al. 2002). However, the reduced abundance of these species in fragment bird communities was counterbalanced by the presence of species that were rare in or

Table 4. Step-wise logistic regression models for the probability of presence of each bird species in forest fragments in relation to the five vegetation structure gradients defined in the Principal Component Analysis (BGROUND, LOWSH,TALLSH, THEIGHT and DENS, see Table 2) and to fragments area (AREA) and proportion of agriculture habitats around the fragment (AGRI). The two latter variables were included after the effect of the habitat variables had been estimated. Degrees of freedom (d.f.), change in deviance (χ^2) from the null to the final model, probability value (*P*) and Nagelkerke's R squared value (R^2) ranging between 0 and 1 are also shown.

Bird species	Variables included in the logistic regression model	d.f.	χ^2	*P*	R^2
Wood Pigeon	–				
Turtle Dove	DENS (+), AREA (−)	1	3.42	< 0.05	0.27
Wryneck	–				
Green Woodpecker	LOWSH(-),THEIGHT (+)	2	11.12	< 0.01	0.39
Common Cuckoo	LOWSH (+), AREA (−)	2	7.24	< 0.05	0.30
Woodlark	AREA (-)	1	6.11	< 0.01	0.30
Wren	TALLSH (+), AREA (+)	2	19.21	< 0.001	0.66
Robin	LOWSH (−)	1	3.26	< 0.1	0.17
Nightingale	LOWSH (+)	1	3.04	< 0.1	0.14
Blackbird	LOWSH (+)	1	4.66	< 0.01	0.38
Bonelli's Warbler	–				
Sardinian Warbler	–				
Firecrest	BGROUND (+), AREA (+)	2	7.76	< 0.01	0.45
Long-tailed Tit	HEIGHT (+), BGROUND (+), AREA (+)	3	9.72	< 0.05	0.69
Spotted flycatcher	AREA (-)	1	3.699	< 0.05	0.19
Crested Tit	AREA (+)	1	5.01	< 0.01	0.23
Coal Tit	AREA (+)	1	4.14	< 0.05	0.34
Blue Tit	DENS (−), TALLSH (+)	2	15.4	< 0.01	0.76
Great Tit	–				
Golden Oriole	LOWSH(+)	1	3.49	< 0.05	0.16
Short-toed Treecreeper	TDENS (+), AREA (+)	2	8.11	< 0.001	0.26
Woodchat Shrike	LOWSH(+), AGRI(+), AREA(-)	3	16.80	< 0.01	0.64
Jay	AREA (+)	1	7.32	< 0.01	0.32
Greenfinch	THEIGHT(-), DENS(+), AREA (-), AGRI(+)	4	15.17	< 0.001	0.68
Goldfinch	THEIGHT (-), LOWSH(-), TALLSH(-), AREA (+)	4	6.80	< 0.01	0.79
Serin	–				
Rock Bunting	BGROUND (+)	1	5.05	< 0.05	0.43
Cirl bunting	AGRI(+)	1	3.87	< 0.05	0.21
Corn Bunting	AREA(-)	1	5.76	< 0.01	0.46

missing from continuous forests. The abundance of most of these species actually increased with decreasing fragment area and was also significantly higher in fragments than in shrublands (Table 3). Landscape heterogeneity as such seems therefore critical in structuring local bird communities by providing suitable conditions to species that would otherwise be more rare or absent (Izhaki and Adar 1997; McCollin 1998; Moreira et al. 2001).

Fragmentation, supplementation and complementation

The limited impoverishment of forest fragments in species characteristic of continuous forest habitats brings only partial support to the *fragmentation* hypothesis and suggests that most species found in continuous forests find the resources they need in forest fragments (but see the argument of Santos et al. 2002 that forest birds most sensitive to fragmentation are missing in the Mediterranean) or are able to find them in the shrublands that surround the fragments (*habitat supplementation* of Dunning et al. 1992 and *habitat compensation hypothesis* of Norton et al. 2001).

Our results support the view that for a number of species, forest fragments may turn out to be important habitats containing resources (food, shelter, etc) not found in either continuous forests or shrubland matrix. Different ecological mechanisms may explain why some are more abundant in forest fragments. First, the higher cover of tall shrubs or the lower tree density in forest fragments when compared to continuous forests may account for some of the differences between different forest types. In some conditions relatively open forests may be enough to allow

the persistence of species such as the Turtle dove (Prodon and Lebreton 1981; Pulido and Díaz 1992). However, most of the species characterising forest fragments are known for their non exclusive use of forest habitats and are dependant to some extent on the proximity of open habitats. The occurrence, in forest fragments, of species absent from continuous forest and from continuous shrublands, strongly suggests that the mosaic of habitats is necessary to their presence (*habitat complementation* hypothesis of Dunning 1992). Species such as the Wryneck, the Spotted flycatcher or some fringilids may typically breed in trees but commonly forage in open habitat (i.e., shrublands) in which some food types may be more common or more easily obtained (Perrins 1998). Other species, such as the Woodlark, which need both trees (as singing perches or as refuge from predators) and more open patches of habitat will be missing from continuous shrublands and from continuous forests (Schaefer and Vogel 2000). The fact that many of these species were more abundant in smaller fragments than in larger ones also suggests an effect of the matrix on their presence. Finally, for some migrant forest species, such as the Golden oriole, the preference for forest patches may be associated to the particular quality of these habitats in which territories are easier to assess and establish (Tye 1992) or cheaper to defend due to a reduction in the number of neighbours in forest patches (Mazerolle and Hobson 2002).

The additional positive effect of agriculture on some species, such as the Cirl bunting or the Goldfinch, is consistent with their dependence on food found in agricultural habitats (Moreira et al. 2001). Both are known to need the presence of trees to breed.

Thus, only a minority of the species observed follow expectations from the *fragmentation hypothesis*. A larger proportion of species follows patterns consistent with the *supplementation* (continuous forest species not affected by fragmentation) / *complementation hypotheses* (species more abundant in the fragments/shrubland matrix complex than in any continuous habitat). These results underline how the response to fragmentation is species specific in these bird communities. They confirm similar conclusions of Debinski and Holt (2000); McGarigal and Cushman (2002) and Bissonette and Storch (2002) and agree with the view that, at local scales, different ecological processes operate simultaneously to determine bird distribution in mosaic landscapes (Dunning et al. 1992; Law and Dickman 1998).

Implication for conservation of bird communities in Mediterranean habitat mosaics

The large-scale abandonment of marginal agricultural lands in the North-eastern Mediterranean basin resulted, in many parts of the northern Mediterranean, in a progressive reduction in open habitats, and/or, in some areas, in forest expansion (Debussche et al. 1999; Preiss et al. 1997). On the basis of our results, such a reduction of landscape heterogeneity by expanding forests may progressively decrease bird diversity in Mediterranean woodlands (Pino et al. 2000), especially given the scarcity of many forest specialists in the region (Santos et al. 2002). Keeping Mediterranean landscapes heterogeneous may necessitate a variety of means including controlled fires or grazing (Hardy and Arno 1996; Izhaki and Adar 1997; Pons 1998). In this context, fire dynamics will play a key role since it has been shown that large scale vegetation recovery often increases frequency of wild fires (Trabaud 1981; Moreira et al. 2001, Lloret et al. 2002). This can be further enhanced by the current trend of warmer summers (Piñol et al. 1998). Natural or human induced fires of moderate size are usually seen as favouring landscape dynamics and heterogeneity (Lloret et al. 2002, Pons et al. 2003). Large fires burning thousands of ha are generally thought to increase landscape homogeneity, but recent studies show that mosaic landscapes combining forest fragments of different tree species and open areas may also originate from large fires burning continuous forest habitats (Retana et al. 2002).

Fragmentation is often associated with impoverished forest bird community (McGarigal and Cushman 2002, but see Fischer and Lindenmayer 2002). However, in Mediterranean areas where wild fires have drastically fragmented and reduced forests, fragments will be critical to keeping a number of bird species. They not only host the remaining forest species, but are also essential for species depending on the mosaic of both forests and open habitats.

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