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Habitat, Landscape and Bird Composition in Mountain Forest Fragments

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The study attempts to separate the effects of forest fragmentation related to landscape (patch area, isolation) and habitat (altitude, vegetation structure) on bird community composition in a mountain pine forest. Bird composition was related, using a multivariate approach (canonical correspondence analyses), to either habitat or to landscape, eliminating the effect of habitat statistically. Bird composition and species richness varied with patch area and isolation from large pine stands, but this effect could be assigned principally to variation in vegetation structure and altitude. Another effect, that of increasing occurrence and numbers of *Anthus trivialis* with decreasing distance to nearest low-altitude forest, could be assigned to both habitat (grass cover) and landscape (connectivity effects). Management implications are drawn from the results.

Keywords: passerines, Pyrenees, *Pinus uncinata*, forest fragmentation, landscape, habitat, point counts, multivariate analysis.

1. Introduction

In most studies investigating the effects of forest fragmentation on bird community composition, "pure" and "biased" effects are not clearly separated (Opdam and Schotman, 1987). We mean by pure effects changes in species composition related to the influence of fragmentation *per se*; that is to say spatial features of the landscape—patch size and isolation—on demographical processes. They include changes due to increase in

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probability of extinction and decrease in probability of immigration, predicted by the insular biogeography theory of MacArthur and Wilson (1967), that prompted many workers to deal with forest fragmentation (e.g. Whitcomb *et al.*, 1981; Harris, 1984; Opdam *et al.*, 1984). They also include changes due to connectivity, that is to say interconnection of sub-populations into a functional demographical unit through spatial closeness of landscape elements (Baudry and Merriam, 1988). By biased effects, we mean those related to habitat variation (altitude and vegetation structure) coinciding with fragmentation (e.g. Connor and MacCoy, 1979). The knowledge of these biased effects is especially relevant for forest management applied to bird conservation.

Models dealing with pure and biased effects together, i.e. based on both habitat and landscape (e.g. Ambuel and Temple, 1983; Cieslak, 1985; Blake and Karr, 1987), may produce confusing results because of high correlations between the two groups of variables (Lynch and Whigham, 1984; Rafe *et al.*, 1985). Situations where the forest tracts can be considered as having the same habitat in spite of size differences are the best for testing the hypothesis of a landscape effect (Morse, 1977; Opdam *et al.*, 1984; Van Dorp and Opdam, 1987). However, such situations are not frequently encountered. Another solution for separating the two types of effect consists in testing for a habitat effect, and for a landscape effect after eliminating the habitat effect statistically.

In this paper we have attempted to separate in this way landscape and habitat effects of forest fragmentation on bird community composition in a coniferous mountain forest. First, we studied the effects of habitat variables upon bird composition. Then, we studied the effects of landscape variables after eliminating habitat effects. To perform these analyses, it was necessary that landscape and habitat might vary to some degree independently from each other, which was verified in our study area. We show how our results can be used by forest managers for the conservation of both rare species and a high species richness.

2. Methods

2.1. STUDY AREA

The study area was situated in the mountain Néouvielle, located in the middle of the French Pyrenees. The climate is oceanic with a continental trend. It is very cold because of the high altitude. Forest occupies 30% of a 1600-km² area centred on the study area. Mountain pines (*Pinus uncinata* Ram.) grow between 1800 and 2400 m.

The extent and pattern of pine forests are limited by geomorphology, altitude, fire and grazing (Cantegrel, 1986). Grazing and fire have influenced vegetation in the Pyrenees for at least 4000 years (Métailié, 1984). As a consequence, pine forests are fragmented into patches of different size, surrounded by a more or less rocky grassland and by heaths. Nowadays, grazing and fire are decreasing and forest colonizes heaths and grasslands. Pine fragmentation in Néouvielle represents a current situation in high-altitude forests. Pine forests are sometimes connected with low-altitude forests, which harbour silver firs (*Abies pectinata* L.), beeches (*Fagus sylvatica* L.) and larch (*Larix decidua* L.).

2.2. SAMPLING

The sampling design ensured that the 58 selected patches represented a large variation in size, distance to the nearest large pine patch and distance to the nearest large patch of

low-altitude forest (here larch or silver fir stands > 300 ha), the latter sharing a pool of species with pine stands. Patches were classified according to size: small woodlots (≤ 2 ha), medium woodlots (2–30 ha) and large stands (> 90 ha). Among large stands, "peninsular" and "continental" parts were distinguished. Peninsular stands had their width smaller than 300 m. Patches with a distance to the nearest patch of low-altitude forest equal to zero were all woodlots; they were called connected woodlots.

Sampling was done during spring 1987 for birds, habitat and landscape variables simultaneously, in each of 58 selected patches on the points of a grid (200×200 m), yielding a total of 195 sampling points. The field work had been prepared on maps, with grids randomly placed on selected woodlots. All the points of grids within the boundaries of medium or small woodlots were sampling points, so that woodlots were saturated with sampling points. Thirty per cent of large stands was sampled on continuous areas. Thus, the numbers of sampling points in either medium–small or large stands were approximately equal.

Bird sampling used the point-count technique (Blondel *et al.*, 1981). Only singing passerines and *Picidae* were counted. Songs were recorded within a radius of 50 m as determined by the size of the smallest pine woodlot.

Classical habitat variables (Table 1) were evaluated in the field, within the 50-m radius used for bird sampling. Per cent cover was estimated by comparison with reference drawings representing imaginary covers of 1, 5, 10% ... (in Prodon and Lebreton, 1981). The values of the landscape variables, describing both patch size and isolation from either large pine stands or low-altitude forest (Table 1), were evaluated from 1/25 000 IGN maps and from 1/20 000 IGN aerial photographs.

TABLE 1. Variables estimated for each sampling point

	Code	Meaning
Habitat (within the listening radius)		
	AL	Altitude (m)
	O†	Cover of within-forest open areas (%)
	S†	Cover of stones (< 0.5 m in diameter) (%)
	B	Cover of boulders (> 0.5 m in diameter) (%)
	L1	Cover of vegetation layer < 0.25 m
	L2†	Cover of vegetation layer 0.25–0.5 m
	L3†	Cover of vegetation layer 0.5–1 m
	L4†	Cover of vegetation layer 1–2 m
	L5	Cover of vegetation layer 2–4 m
	L6	Cover of vegetation layer 4–8 m
	L7†	Cover of vegetation layer 8–16 m
	L8†	Cover of vegetation layer > 16 m
	CH†	Canopy height (m)
	DT†	Number of dead trees
Landscape		
	A	Forest patch area
	DP†	Distance to the nearest large pine stand (km)
	DLA	Distance to the nearest low-altitude forest (km)

† Log-transformed ($\log(x+1)$ or $\log^2(x+1)$).

‡ Square root-transformed ($(x+1)^{1/2}$).

2.3. STATISTICAL ANALYSES

Bird composition patterns were related to explanatory variables (habitat and/or landscape) through canonical correspondence analyses (Ter Braak, 1986) on the couples of tables, $T1$ = sampling points \times bird species (counts), $T2$ = points \times explanatory variables (values). Casual species (≤ 3 contacts on the total of 195 sampling points) were removed for statistical reasons, as well as two open-area species, *Phoenicurus ochruros* L. and *Anthus spinoletta* L., which were contacted during the census. These two species could potentially bias analyses concerning forest patches.

Canonical correspondence analysis performs a correspondence analysis of the projection of $T1$ on the vectorial subspace generated by $T2$ (Lebreton *et al.*, 1988), so that bird community variation can be related to external variables (Ter Braak, 1986). The $T1$ variance can be decomposed according to various subspaces (Sabatier *et al.*, 1989). We first considered the subspace generated by both landscape and habitat ($L + H$) able to express global fragmentation effects. This subspace was decomposed into a subspace generated by habitat alone (H) and a subspace generated by landscape with habitat effects partialled out (L/H) (Sabatier *et al.*, 1989). Thus, three canonical correspondence analyses were performed, on the couples ($T1, L + H$), ($T1, H$) and ($T1, L/H$), respectively. In the last analysis, the values of the p landscape variables with q partialled-out habitat covariables were residuals of multivariate multiple linear regressions of the p raw variables on the q raw variables (Ter Braak, 1988). Some variables were log- or square-root-transformed to reduce skewness (Table 1). Interpretation of results was based on the following, as recommended by Chessel *et al.* (1987) and by Lebreton *et al.* (1988): (1) eigenvalues and decomposition of variance according to highest-ranking factors; (2) patterns of points and species on the factor planes; (3) circle of correlations between explanatory variables and factors.

Classical parameters were also calculated for a comparison according to patch size or connection with low-altitude stands. No comparison according to distance to the nearest large pine stand was done because of a redundancy with patch size ($r = 0.71$, $P < 0.001$). Total species richness was estimated in each patch class from accumulation curves, as recommended by Verner (1986), the obtained value being fitted to the MONOD function, as proposed by Lauga and Joachim (1987). The function estimates total richnesses in patches sampled with different sampling efforts. An index of bird abundance was assessed in each patch class as mean numbers of individuals per point. The bird species were distributed after G  roudet (1974, 1980a,b) among the following groups: forest species, edge species, open-area species. The proportion of any of these groups in the bird community was calculated on the basis of bird abundance indices. These avifauna parameters were compared between classes of patch size using Kruskal-Wallis tests followed by 0.05 Noether tests (1976 in Scherrer, 1984) if the null hypothesis was rejected, and according to connection with low-altitude stands using Mann-Whitney tests.

The multivariate analyses were performed with the statistical package BIOMECO (Lebreton *et al.*, 1987).

3. Results

3.1. EFFECTS OF FRAGMENTATION ON BIRD COMPOSITION PATTERNS, ASSESSED BY HABITAT AND LANDSCAPE

The two first factors of the canonical correspondence analysis involving habitat and

landscape variables (eigenvalues 0.180 and 0.111) accounted for 61% of the data variance. The pattern of points on *F1* indicated a gradient from points of small woodlots to points of "continental stands", points of medium woodlots and "peninsular surveys" being intermediate [Figure 1(a)]. Distance to the nearest large pine stand decreased along this gradient [Figure 1(c)]. At the ends of the gradient, one found *Anthus trivialis* L., *Turdus torquatus* L., *Serinus citrinella* L. and *Prunella modularis* L. (negative scores) as opposed to *Garrulus glandarius* L., *Certhia familiaris* L., *Dendrocopos major* L., *Motacilla cinerea* L. and *Troglodytes troglodytes* L. [positive scores; Figure 1(b)]. We also noticed along the gradient described by *F1* no significant change in bird abundance, but an increase in species richness, an increase in the ratio of forest species, a decrease in the ratio of edge species and a decreasing tendency for open-area species (Table 2). *F2* opposed medium and small woodlots isolated from low-altitude stands (positive scores) to those connected with such stands (negative scores) [Figure 1(a) and (c)]. The points of connected woodlots were accompanied by *Anthus trivialis*, as opposed to the other species [Figure 1(a) and (b)]. Bird abundance and ratio of edge species were higher in connected woodlots than in unconnected woodlots, whereas no change in species richness was noticeable (Table 3).

Fairly high correlations between habitat and landscape variables naturally obscured the respective role of the two types of variables in the explanation of the plane pattern [Figure 1(c)]. For example, large patches were associated with low altitudes and high canopies [Figure 1(c)].

The following factors of the canonical correspondence analysis were not studied because they were not related to fragmentation features.

TABLE 2. Bird community parameters along a gradient from small woodlots to continental stands (first axis *F1* of the canonical correspondence analysis involving habitat and landscape variables)

	Small woodlots (≤ 2 ha) (1)	Medium woodlots (2–30 ha) (2)	Large stands		Kruskal-Wallis test	Noether test
			Penins. (> 90 ha) (3)	Contin. (4)		
						$> F1$
Total richness (estimate)		15	16	18	—	—
Total abundance (mean number of individuals per point count)	6.2	7.4	7.4	7.8	n.s.	—
Percentage of birds relative to habitat						
Forest species	51.9	62.5	66.7	78.7	***	1 < 4* 2 < 4* 3 < 4*
Edge species	29.5	26.1	29.2	17.8	**	1 > 4* 2 > 4* 3 > 4*
Open-area species	18.6	11.4	4.1	3.5	n.s.	—

n.s., not significant; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

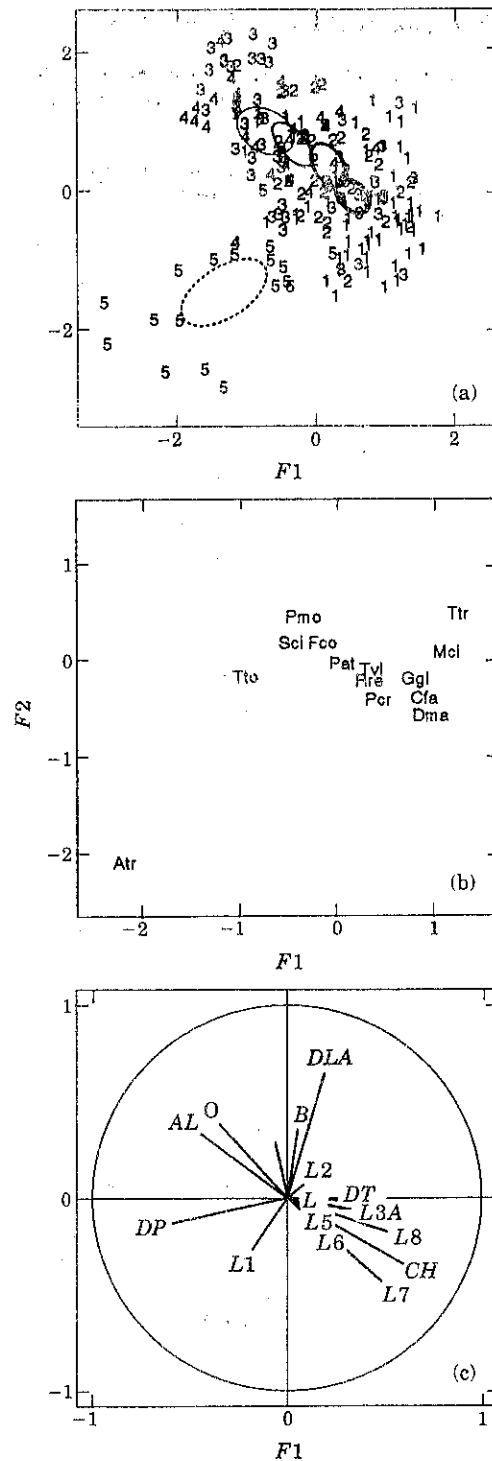


Figure 1. $F1 \times F2$ plane of the canonical correspondence analysis involving habitat and landscape variables. (a) Projection of points with 95% confidence ellipses for five groups (1, points of "continental" stands; 2, points of "peninsular" stands; 3, points of medium woodlots; 4, points of small woodlots, with decreasing thickness of line for confidence ellipses from 1 to 4; 5, points of woodlots connected with low-altitude stands—dotted line). (b) Scores of species. Atr: *Anthus trivialis*, Cfa: *Certhia familiaris*, Dma: *Dendrocopos major*, Fco: *Fringilla coelebs*, Ggl: *Garrulus glandarius*, Mcl: *Motacilla cinerea*, Pat: *Parus ater*, Pcr: *Parus cristatus*, Pmo: *Prunella modularis*, Rre: *Regulus regulus*, Sci: *Serinus citrinella*, Tto: *Turdus torquatus*, Ttr: *Troglodytes troglodytes*, Tvi: *Turdus viscivorus*. (c) Correlation plot of habitat and landscape variables.

TABLE 3. Bird community parameters according to connection with low-altitude stands (second axis $F2$ of the canonical correspondence analysis involving habitat and landscape variables)

	Medium or small woodlots		Mann-Whitney test → $F2$
	Connected (C)	Unconnected (UC)	
Total richness (estimate)	15	14	—
Total abundance (mean number of individuals per point count)	10.3	7.4	$C > UC^*$
Percentage of birds relative to habitat			
Forest species	54.8	61.4	n.s.
Edge species	37.7	23.4	$C > UC^*$
Open-area species	7.5	15.2	n.s.

n.s., not significant; *, $P < 0.05$.

3.2. SEPARATION OF HABITAT AND LANDSCAPE EFFECTS

The two first factors of the canonical correspondence analysis involving habitat variables alone accounted for 61% of the data variance. The point and bird patterns on the $F1 \times F2$ plane resembled those of the previous analysis [Figure 2(a) and (b)]. The pattern on $F1$ was explained by a set of intercorrelated variables, i.e. altitude (AL) and within-forest open-area cover (O), both negatively correlated to $F1$, canopy height (CH) and cover of high vegetation layers ($L7$, $L8$), both positively correlated to $F1$ [Figure 2(c)]. Thus, $F1$ was a gradient from edge to forest species expressing the effect of changes in vegetation structure and altitude. From the Figure 2(a), these changes coincided with increasing patch size and decreasing isolation from large pine stands. The pattern on $F2$ was explained by an opposition between boulder cover (B) and grass cover ($L1$) [Figure 2(c)]. From Figure 2(a), distance to low-altitude stands increased with $F2$ scores.

The two first factors of the canonical correspondence analysis involving landscape variables with habitat effects partialled out accounted for 90% of the data variance. $F1$ isolated points of woodlots connected with low-altitude stands [Figure 3(a)]. Distance to the nearest low-altitude stand (DLA) explained this pattern [Figure 3(c)]. $F1$ expressed the same general sense as the second factor of the canonical correspondence analysis involving habitat and landscape variables. As on this previous factor, *Anthus trivialis* was opposed to the other species. *Turdus torquatus* was affected (to a lesser extent) by the same tendency [Figure 3(b)]. $F2$ opposed points of large pine stands to points of medium or small woodlots isolated from large pine stands [Figure 3(a)]. Patch area (A) and distance to the nearest large pine stand (DP) explained this pattern [Figure 3(c)]. $F2$ expressed the same general sense as the first factor of the canonical correspondence analysis involving habitat and landscape variables, though it was an opposition rather than a gradient. The species pattern was different from those on the analogous factors of the previous analyses. Five species notably characterized the factor, *Garrulus glandarius* and *Dendrocopos major* for large pine stands, and *Prunella modularis*, *Anthus trivialis* and *Troglodytes troglodytes* for small woodlots [Figure 3(b)].

Among the two factors linked to patch area and isolation from large pine stands, $F1$ of the analysis involving habitat variables and $F2$ of the analysis involving landscape variables with habitat effects partialled out, only the first one accounted for a high part of

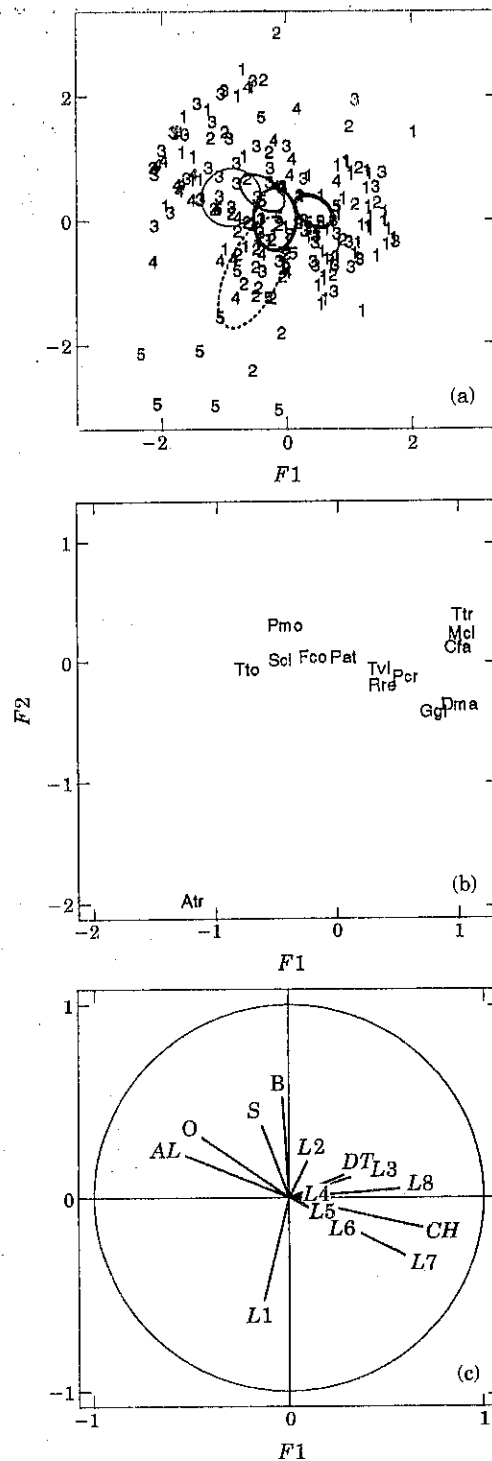


Figure 2. $F1 \times F2$ plane of the canonical correspondence analysis involving habitat variables. (a) Projection of points with 95% confidence ellipses for the same five groups as in Figure 1. (b) Scores of species. (c) Correlation plot of habitat and landscape variables.

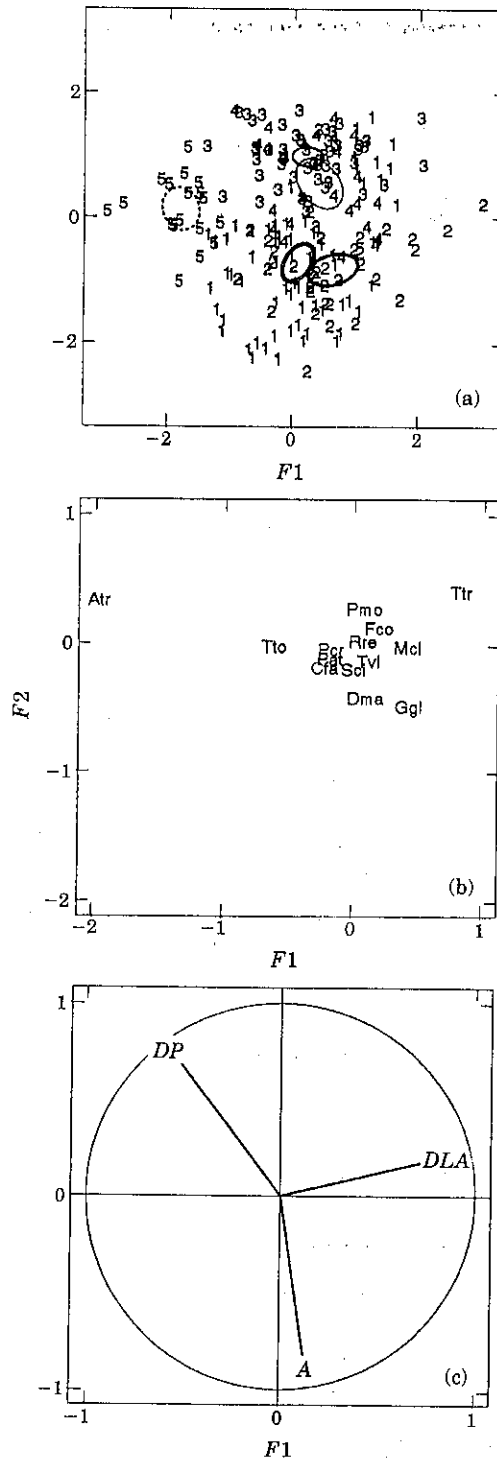


Figure 3. $F1 \times F2$ plane of the canonical correspondence analysis involving landscape variables with habitat partialled out. (a) Projection of points with 95% confidence ellipses for the same five groups as in Figure 1. (b) Scores of species. (c) Correlation plot of habitat and landscape variables.

the data variance (eigenvalue = 0.162 vs. 0.019). Thus, habitat alone was sufficient for explaining the effect of patch area and isolation from large pine stands on bird composition.

The two factors linked to isolation from low-altitude forest, *F2* of the analysis involving habitat variables and *F1* of the analysis involving landscape variables with habitat effects partialled out accounted for the same part of the data variance (eigenvalue = 0.066 vs. 0.069). Thus, habitat and landscape variables were both important for explaining the effect of isolation from low-altitude forest on bird composition.

4. Discussion

The most important fragmentation effect on bird composition in our study area was apparently related to both patch area and isolation from large pine stands. Species richness decreased with decreasing patch size and increasing isolation, as has been observed before (Forman *et al.*, 1976; Whitcomb *et al.*, 1981; Lynch and Whigham, 1984). However, total bird abundance did not change according to patch size and isolation. The maintenance in forest islands of bird densities as high as in large pine stands despite lower species richness was due to the low densities of species occurring only in large pine stands. The ratio of edge species increased along the same gradient, as in other situations (Howe, 1984; Nilsson, 1986; Blake and Karr, 1987).

This effect corresponded principally to a biased one, that of increasing altitude and changes in vegetation structure (vertical structure, within-forest open-area cover) coinciding with fragmentation. On the one hand, decreasing species richness with increasing altitude is well known (MacArthur, 1972; Blondel, 1978). On the other hand, fragmentation was also associated with decreasing vertical habitat diversity through decreasing cover of high vegetation layers. Such a phenomenon may explain an important part of decreasing species richness, following several authors (Lynch and Whigham, 1984; Cieslak, 1985; Helle, 1985; Freemark and Merriam, 1986; Boecklen, 1986). The high ratio of edge species in small woodlots may be due to the high cover of small patches of open areas in these woodlots, allowing species such as *Serinus citrinella* to colonize through the juxtaposition of two biotopes, or favouring species such as *Prunella modularis* through the creation of a complex new biotope (Frochot, 1981, 1985). The parallel increasing tendency for open-area species supports this hypothesis.

However, a slight effect of patch area and isolation from large pine stands was demonstrated with habitat effects partialled out. Large pine stands appeared to favour especially *Dendrocopos major* and *Garrulus glandarius*, two large species requiring territories of sufficient size. *Prunella modularis*, *Anthus trivialis* and *Troglodytes troglodytes*, three species requiring small territories, appeared to be favoured by medium or small woodlots isolated from large pine stands.

The second fragmentation effect apparently corresponded to the distance to low-altitude forest (firs and larches). Bird abundance increased in woodlots connected to such stands. Such an effect of proximity on abundance was noted by Szaro and Jakle (1985) when studying a desert bird community near a riparian forest. This effect was attributed to both habitat (grass cover) and landscape. It was expressed essentially through occurrence and numbers of *Anthus trivialis*, and to a lesser extent of *Turdus torquatus*, two species abundant in larches (Lebreton *et al.*, 1976; Lebreton, 1984). *Anthus trivialis* is probably favoured by the increase in grass cover coinciding with decreasing distance to low-altitude forest, but we may suggest also a connectivity effect (Forman and Godron, 1986; Baudry and Merriam, 1988).

The consideration of other habitat and landscape variables likely to explain the effect

of fragmentation on birds might partially challenge these results. However, at this point, we conclude that there was only a slight pure effect of area and isolation from large pine stands on birds in our study area. Authors reporting findings similar to ours (Lynch and Whigham, 1984; Haila, 1986) studied avifauna in heavily-forested environments, like ours. Results contrary to ours, such as a strong area and/or isolation effect (Howe, 1984; Blake and Karr, 1987), come from lightly-forested study areas. The most noticeable landscape effect was that of connection with low-altitude stands, which concerned few species.

Finally, management decisions can be helped by our results. First, fragmentation was shown to favour rare species, such as *Serinus citrinella* and *Turdus torquatus*, through edge effects, whereas large stands harbour a high species richness and forest species relatively uncommon in mountain pine and common elsewhere. Second, the proximity of firs and larches was found to cause the occurrence of *Anthus trivialis* and to favour the rare *Turdus torquatus*. Thus, large mountain pine stands with a large edge length, not too far from firs and larches, would favour both rare mountain pine species and a rich forest community. As already pointed out, grazing and fire are decreasing nowadays in the Pyrenees, giving rise to forest colonization, but at the same time the mountain pine forest is still heavily fragmented. Thus, at the moment, the increase of forest area is compatible with the increase of large edge lengths. In the present context of forest colonization, forest managers should favour edge effects and large forest stands for bird conservation purposes.

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