

VEGETATION STRUCTURE IN BEECH-FIR FORESTS:
EFFECTS ON THE AVIAN COMMUNITYSara SÁNCHEZ^{1*}, José Javier CUERVO^{1,2} & Eulalia MORENO¹

RÉSUMÉ.— *Structure de la végétation en hêtraies-sapinières : effets sur le peuplement d'oiseaux.*— Entre mai 2001 et mars 2002, la structure et la composition de la végétation, ainsi que les paramètres de la communauté d'oiseaux (richesse et abondance) dans les forêts mixtes entretenues de hêtres et de sapins (*Fagus sylvatica* – *Abies alba*) de Navarre (nord de l'Espagne) ont fait l'objet d'une étude. Les relations entre les paramètres des oiseaux et les variables de la végétation différaient entre divers groupes d'oiseaux en fonction de leurs habitudes de nidification. Les paramètres des oiseaux utilisant les trous d'arbre pour nicher n'ont montré aucune relation avec les variables de la végétation ; en revanche l'abondance tout comme la richesse des espèces ne dépendant pas des trous d'arbre pour se reproduire affichaient une relation positive avec la proportion de sapins, mais uniquement en période de reproduction. Cette relation pourrait s'expliquer par la sélection du lieu de nidification, les sapins offrant des lieux plus appropriés à la nidification que les hêtres pour ce groupe d'oiseaux, peut-être parce que les feuilles des hêtres ne sont pas entièrement développées au début de la saison de reproduction. En outre, en hiver la richesse des espèces ne dépendant pas des trous d'arbre pour nicher était en relation positive avec la proportion d'arbustes. Bien que ce résultat doive être interprété avec prudence, la protection vis-à-vis des conditions météorologiques défavorables ou les prédateurs pourrait expliquer cette relation.

SUMMARY.— Vegetation structure and composition, and parameters of the bird community (richness and abundance) were studied in managed beech-fir forests in Navarre (Spain). Relationships between bird parameters and vegetation variables differed in different avian nesting guilds. Whereas secondary cavity-nesting bird parameters were not significantly related to any vegetation variable, both richness and abundance of bird species that do not rely on existing holes for breeding increased with the proportion of fir trees, but only in the breeding season. Nest-site selection might be the key factor behind this relationship, since firs would provide more suitable nest-sites than beeches for these species, perhaps because beech leaves are not fully developed early in the breeding season. Moreover, during the winter season richness of birds that do not rely on existing holes for breeding was positively related to the percentage of shrub cover. Although this result should be considered with caution, protection from adverse weather conditions or predation might explain this relationship.

The beech-fir (*Fagus sylvatica* – *Abies alba*) forest is a highly complex ecosystem, with one of the highest levels of organization, productivity and biological value within temperate regions woodlands (Elósegui *et al.*, 1989; Costa *et al.*, 2001). This kind of forest reaches its south-western distribution limit in the Iberian Peninsula where different silviculture systems are used for every tree species. The “even successive thinning” applied to beeches consists of

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a series of cuttings until the trees reach a specific age (characterized by optimal size, soundness, and quality). The stands are then harvested leaving scattered numbers of trees to provide the seeds needed for regeneration. Once new beeches have grown, the seed-trees are also harvested. The objective of this system is to create an evenly-aged stand. In contrast, a mixed treatment is applied to firs, mainly to obtain large trees (Simon *et al.*, 2001).

In Iberian beech-fir forests, the beech is generally more abundant than the conifer (Costa *et al.*, 2001) due to selective extraction of the fir in the past and the strong regeneration capacity of the beech. In addition, fir trees are severely affected by two diseases. The first one is caused by a rust fungus, *Melampsorella caryophyllacearum*, and is characterized by the presence of swellings in trunks and branches. In 2003, about 40 % of fir trees were infected by *M. caryophyllacearum* in Irati forest (Solla & Camarero, 2006). The second disease is the decline syndrome, characterized by symptoms such as defoliation or dryness. Decline syndrome hampers the spread of firs and, in fact, is a threat to fir conservation in the Southern Pyrenees (Camarero *et al.*, 2004). Both diseases are contributing to destabilize the equilibrium between firs and beeches, and favouring a monospecific beech forest.

Vegetation structure (e.g., percentage of plant cover, stem density, height of trees, or amount of dead wood) indicates the suitability of a territory for breeding, sheltering and feeding, and is a primary factor in habitat selection by vertebrates in general and by birds in particular (Hildén, 1965). Although vegetation structure has been traditionally considered as one of the most important factors affecting avian community parameters (MacArthur & MacArthur, 1961; Blondel *et al.*, 1973), bird distribution is not only influenced by vegetation structure, but also by plant species composition (Holmes & Robinson, 1981; Rotenberry, 1985).

The goal of this study was to identify the characteristics of the beech-fir forest related to the richness and abundance of birds. Given the number of threats firs are facing nowadays in Iberian beech-fir forests (see above) and since forest management may help to control fir diseases (Oliva & Colinas, 2007), our attention focused especially on the relationship between fir abundance and avian parameters.

MATERIALS AND METHODS

STUDY AREA

Fieldwork was conducted in Irati, a managed beech-fir forest in the north of Navarre, Spain (42°58'-43°00'N, 1°01'-1°06'W; 1078-1190 m a.s.l.) between May 2001 and March 2002. Irati is the largest (about 17 200 ha) beech-fir forest in the Iberian Peninsula. The climate in the area is Pyrenean with strong oceanic influence (Elósegui *et al.*, 1989).

Fifteen plots at least 200 m apart, but usually more than 500 m apart, were selected, trying to include the maximum range of fir proportion (0-77 % of fir cover). Plots with a larger proportion of firs were not found. The 15 plots were part of a large forest area (i.e., they were not located in isolated fragments), and they were not close to the edges of the forest (the minimum distance between forest edges and study plots was 500 m). All plots included large trees, apparently representing old-growth forest. Every plot was a 25 m-radius circle (i.e., 0.20 ha), and vegetation was sampled only inside the plots. All trees (≥ 10 -cm-diameter at breast height (DBH) and > 3 -m tall), dead or alive, were counted, species identified, and their height and DBH recorded. Height was measured with a clinometer.

Volume of dead wood was calculated as the sums of the volume of snags, stumps and lying dead wood. Lying dead wood was estimated by the Line Intersected Sampling Method (Marshall *et al.*, 2000). State of decay of dead wood was also recorded (Maser *et al.*, 1979; Goodburn & Lorimer, 1998; Pyle & Brown, 1998). Vegetation profiles were made at 16 points in each forest plot, half of which were placed 10 m and the other half 20 m from the centre of the plot, on 8 axes that crossed the centre at 45° angles to each other. At each point, plant species were identified and measured. This allowed the percentage of the plot covered by herbaceous vegetation (< 0.5 -m high), shrubs (0.5-3-m high) or saplings (young trees with a DBH < 10 cm) to be estimated.

BIRD CENSUSES

Bird censuses were conducted at two different times of the year, roughly corresponding to different periods in bird life cycle: breeding (May-June) and wintering (January-March). They were made in the same 15 plots where vegetation structure and composition were studied. The point-count method was employed because it seems the most suited method for forest birds in dense and homogeneous areas as it was the case here (Blondel *et al.*, 1970, 1981; Bibby *et al.*, 2000; Gibbons & Gregory, 2006). Each observation period consisted of 15 minutes and only birds detected

25 m away from the observer or closer were used for analyses (Gibbons & Gregory, 2006; Sánchez *et al.*, 2007). The observer waited for 5 minutes after arrival at the census point, allowing birds to return to their normal activities, before beginning to count the observation time itself. All birds seen or heard were recorded. Every single bird was considered an observation regardless of its territorial status. Two censuses on different days were taken for each plot and period of the year with the exception of four plots during the winter period when only one census was taken per plot due to unfavourable weather. Where data from two censuses were available, mean values were used for each plot and period. All observations were made in the morning (05:15-10:20 h GMT), by the same person (S. S.), and under similar weather conditions, discarding foggy, windy and rainy days.

Avian richness and abundance were calculated using birds both seen and heard, because these figures are closer to the real number of individuals and species present in each plot. However, some biases may have arisen due to differences in density of vegetation among plots or period of the year, leading to differences in visibility (beeches lose their leaves in winter). Avian community parameters were therefore recalculated using only birds heard in the censuses, thus avoiding any possible visibility bias. Results including only birds heard (not shown for brevity) were qualitatively similar to results including birds both seen and heard (see Results). Some biases may have also arisen because birds exhibit different behaviour during the breeding and the winter periods, and differences in behaviour may result in differences in detectability (Roberts & Schnell, 2006). For example, some bird species form flocks or sing less during winter. However, these biases probably are not important in our case, because the smaller the size of the plots, the smaller the bias in detectability due to bird behaviour, and forest plots in our study were quite small (0.20 ha).

Species that rely on existing holes for breeding (secondary cavity-nesting birds) and species that do not rely on existing holes (non-cavity-nesting birds and woodpeckers) have been studied separately because tree holes are expected to be limited in temperate regions under intense forest management (Newton, 1994) and because broad-leaved trees and conifers presumably differ in the availability of nesting holes (Sandström, 1992). All bird species recorded and their nesting guild are shown in the Appendix.

DATA ANALYSIS

Data obtained from the censuses (i.e., number of bird species and individuals recorded during 15 min in 0.20-ha forest plots), enabled two bird community parameters to be calculated for every forest plot and season: richness (mean number of avian species) and abundance (mean number of individuals). All avian and vegetation parameters were approximately normally distributed without transformation (Kolmogorov-Smirnov test, $P > 0.20$). Since mean tree height and DBH were strongly correlated (Pearson correlation, $r = 0.663$, $n = 15$, $P = 0.0071$), we proceeded to a Principal Components Analysis (PCA) and used the first factor resulting from this PCA as a measure of tree size in subsequent analyses. Similarly, volume and state of decay of dead wood were also strongly correlated ($r = 0.789$, $n = 15$, $P < 0.001$), and the first factor from a PCA was used as a measure of dead wood. Trees present in the studied plots were almost exclusively firs and beeches and, consequently, proportion of firs and proportion of beeches were complementary variables ($r = 0.999$, $n = 15$, $P < 0.001$). Thus, only proportion of firs was included in the analyses.

We first determined the best-fit model of vegetation parameters (number of trees, mean tree size, dead wood, percentages of herbaceous vegetation, shrubs and saplings, and proportion of firs) explaining variation in avian parameters by using Akaike's information criterion (AIC; Burnham & Anderson, 2002) in General Linear Models (normal distribution and link function identity). The model with the lowest AIC (corrected for sample size, see Burnham & Anderson, 2002) was considered the most parsimonious and plausible. In all cases the best (most parsimonious) model included a single vegetation variable (see Results). Avian parameters were then regressed on the vegetation variable included in the best model to test for relationships. In this study we performed multiple statistical tests, and it is well known that the risk of incurring Type I error increases with the number of tests performed. To alleviate this problem, we used sequential Bonferroni correction (Rice, 1989), but with a 10 % level of significance to decrease the risk of incurring Type II error (Chandler, 1995). The number of tests included in the correction was $k = 6$ (for correlations between proportion of firs and the other vegetation variables) or $k = 8$ (for relationships between avian community parameters and vegetation variables: 2 seasons \times 2 nesting guilds \times 2 avian parameters). All statistical analyses were performed with the Statistica (StatSoft, 2007) programme.

RESULTS

Firs and beeches did not differ significantly in height, DBH or state of decay within forest plots (paired-t tests; $n = 13$, $-1.12 \leq t \leq -0.87$, $P \geq 0.28$ in the three cases). Moreover, proportion of firs was not significantly correlated with any of the other vegetation variables (total number of trees, tree size, dead wood, and percentage of herbaceous vegetation, shrubs and saplings; Pearson correlations, $n = 15$, $-0.25 \leq r \leq 0.51$, $P \geq 0.051$ in the 6 tests), suggesting that vegetation structure did not depend on fir abundance. Table I summarizes vegetation characteristics in the 15 studied forest plots.

A total of 22 bird species were recorded in our censuses, 21 in the breeding period and 16 in the wintering period (see the Appendix). Mean richness and abundance of the two nesting guilds (birds that do not depend on existing holes for breeding and secondary cavity-nesting birds) during the breeding and the winter seasons are shown in Table II. Both abundance and

richness of birds that do not depend on existing holes for breeding were positively related to the proportion of firs in the breeding season (Tab. III, Fig. 1) and to the percentage of shrubs in the winter season (Tab. III, Fig. 2), although the relationship between abundance of birds and shrubs in winter was non-significant after sequential Bonferroni correction (Tab. III). Regarding secondary cavity-nesting birds, neither abundance nor richness was significantly related to any vegetation variable after sequential Bonferroni correction (Tab. III).

TABLE I

Mean, standard error (SE) and range of vegetation characteristics in 15 plots of Irati beech-fir forest. For an explanation of vegetation variables and plot characteristics see the text

Vegetation variable	Mean	SE	Range
Number of trees	117.9	12.8	71 - 244
DBH (cm)	30.0	2.1	18.4 - 47.0
Height (m)	20.4	0.9	15.2 - 27.6
Dead wood volume (m ³)	10.6	2.3	1.7 - 32.6
Stay of decay of dead wood	2.0	0.1	1.2 - 3.3
Percentage of herbaceous vegetation	21.3	5.9	0 - 62.5
Percentage of shrubs	11.7	3.7	0 - 43.8
Percentage of saplings	8.3	2.5	0 - 31.3
DBH of beeches (cm)	27.9	3.0	16.7 - 57.4
DBH of firs (cm)	32.3	2.1	18.9 - 44.2

TABLE II

Mean (SE) and range of richness (number of species) and abundance (number of individuals) in secondary cavity-nesting birds and birds that do not rely on existing holes for breeding for two different seasons (breeding and wintering) in 15 forest plots. For census and plot characteristics see the text

Nesting guild	Season	Richness		Abundance	
		Mean (SE)	Range	Mean (SE)	Range
Birds that do not rely on existing holes for breeding	Breeding	3.90 (0.33)	2.0 - 5.5	6.83 (0.65)	3.5 - 11.0
	Winter	2.10 (0.27)	0.5 - 5.0	4.13 (0.47)	1.0 - 9.0
Secondary cavity-nesting birds	Breeding	1.77 (0.19)	0.5 - 3.0	2.43 (0.31)	0.5 - 4.5
	Winter	1.93 (0.29)	0.0 - 4.0	3.00 (0.59)	0.0 - 8.5

DISCUSSION

The proportion of firs in our beech-fir forest was the only vegetation characteristic related to richness and abundance of birds during the breeding season, specifically in bird species that do not depend on existing holes for nesting. Previous studies have found that forests with greater structural complexity and a larger number of plant species are richer in avian communities (Wilson, 1974; James & Warmer, 1982; Easton & Martin, 1998; Poulsen, 2002), because they provide a wider range of niches for feeding or breeding. Vegetation structure has been more intensively studied in relation to bird community than species composition of forests because it has been traditionally considered a more important factor in explaining bird distribution (Blondel *et al.*, 1973; MacArthur & MacArthur, 1961; Willson, 1974; James & Warmer, 1982; DeGraaf *et al.*, 1998). In our study, however, the variation in the proportion of the two main trees species (firs and beeches) seemed to be an important factor in explaining bird community characteristics in the forest.

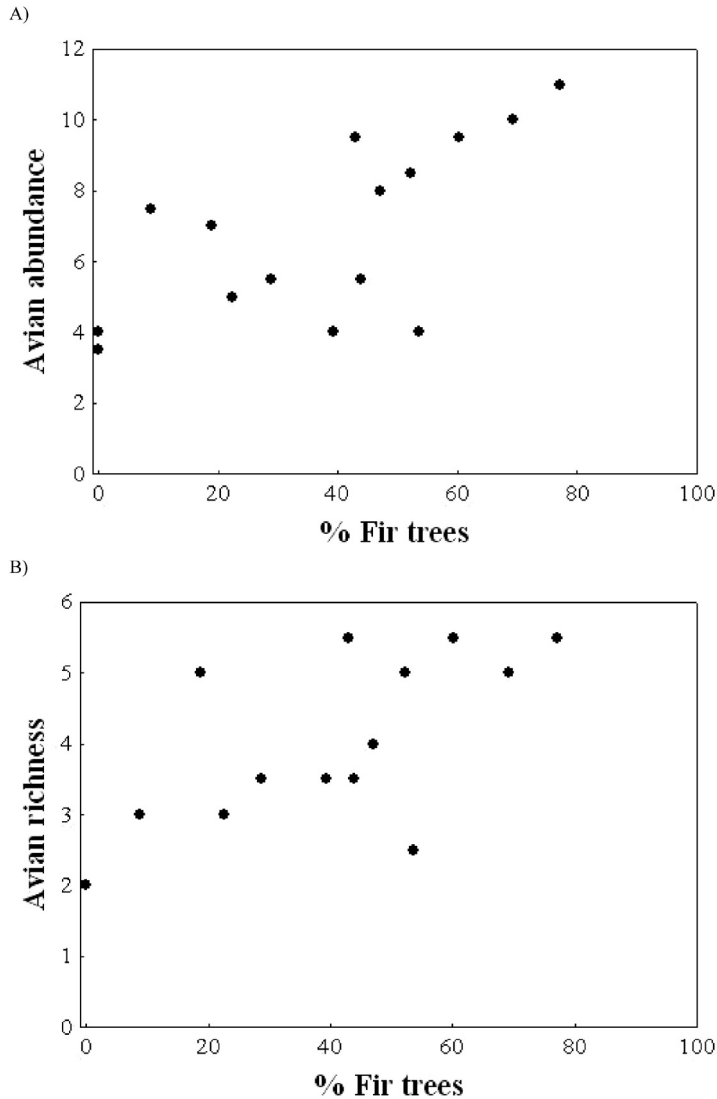


Figure 1.— Relationship between mean (A) abundance and (B) richness of bird species that do not depend on holes for breeding and proportion of firs in beech-fir forest plots during the breeding season. Statistical values are given in Table III.

This study found that the proportion of firs (in relation to beeches) had a positive effect on some avian parameters. However, since there were no forest plots with firs only, we do not know if a pure fir forest would be richer in number of bird individuals or species than a mixed fir-beech forest. Consequently, two scenarios are possible. Firstly, our results could be explained simply if mixed fir-beech forests were better habitats for birds than monospecific forests, regardless of the tree species (Blondel, 1987; Hobson & Bayne, 2000). Secondly, it might be possible that firs provided a better habitat for birds than beeches. Pure fir forest is an environment of low structural diversity (Costa *et al.*, 2001), and this may suggest a lower diversity of birds than a mixed forest (Purroy, 1971; Vilá & Rodríguez-Tejeiro, 1992) although higher than artificial coniferous plantations (Lebreton & Pont, 1987; Lebreton, 1991). Consequently, we can speculate that the first scenario is more plausible.

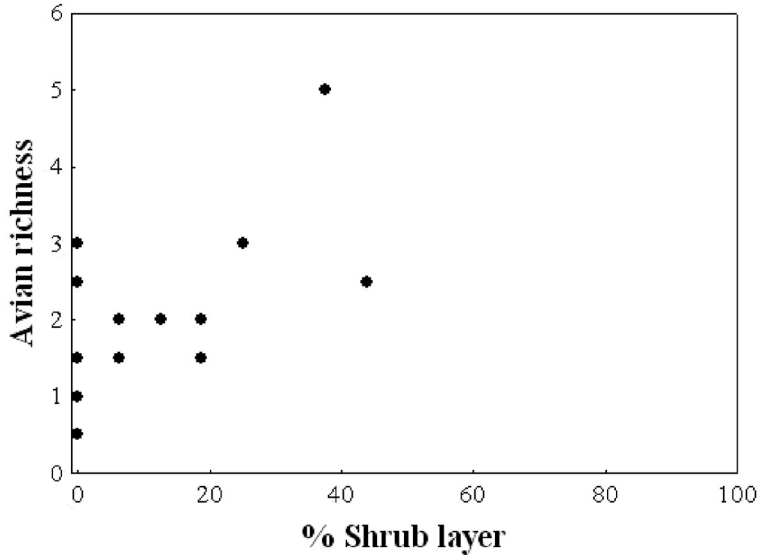


Figure 2.— Relationship between mean richness of bird species that do not depend on holes for breeding and percentage of shrubs in beech-fir forest plots during the winter season. Statistical values are given in Table III.

TABLE III

Regressions between avian community parameters and vegetation variables from best models (determined by using AIC, see the text) in breeding and winter season for two avian nesting guilds. * Statistically significant after sequential Bonferroni correction (see the text for details)

Nesting guild	Season	Avian parameter	Vegetation parameter	Adjusted-r ²	F _{1,13}	P
Birds that do not rely on existing holes for breeding	Breeding	Abundance	Proportion of firs	0.409	10.69	0.0061*
		Richness	Proportion of firs	0.456	12.75	0.0034*
	Winter	Abundance	Percentage of shrubs	0.252	5.72	0.0326
		Richness	Percentage of shrubs	0.324	7.72	0.0157*
Secondary cavity-nesting birds	Breeding	Abundance	Percentage of shrubs	0.044	1.65	0.2214
		Richness	Percentage of shrubs	0.212	4.77	0.0478
	Winter	Abundance	Mean tree size	0.173	3.93	0.0689
		Richness	Number of trees	0.142	3.33	0.0913

It is commonly assumed that cavity-nesting bird species are seriously limited by the availability of tree holes in managed forests (Hildén, 1965; Newton, 1994). Our results suggest that fir/beech proportion does not affect the availability of nesting holes, thus contradicting previous studies suggesting different availability of nesting holes in broad-leaved trees and conifers (Sandström, 1992). One possible explanation for this finding might be that cavity-nesting birds show certain plasticity in nest-site selection and can breed not only in typical tree holes, but also in stumps and in cavities formed by roots (Monrós *et al.*, 1999; Roberge & Månsson, 2003). Moreover, Irati forest is a region where most of the woodpeckers of the Iberian Peninsula are present (Elósegui, 1985; Garmendia *et al.*, 2006). It is known that holes

of woodpeckers are reused by secondary cavity-nesting birds unable to excavate their own nests (Newton, 1994; Aitkinen *et al.*, 2002; Remm *et al.*, 2006). Although woodpeckers often prey on nestlings of other species (Walankiewicz, 2002), they are not generally considered to be important predators of birds (del Hoyo *et al.*, 2002). The presence of a well-conserved woodpecker population, together with the fact that all study plots represented an old-growth forest would increase the availability of holes for cavity-nesting birds in both firs and beeches, and tree holes might not be a limited resource in the studied forest.

Mixed-species forests usually provide increased foraging opportunities for birds either in terms of seed and fruit production or because of the invertebrate communities present in different tree species (Camprodon, 2001). However, Peck (1989) and Adamík & Korňan (2004) found that birds underuse certain tree species, like beeches for instance, when foraging due to the low quality (in terms of food abundance; see Suorsa *et al.*, 2004) of that particular habitat. The main nourishment supplied by beech trees is beech mast, since insect biomass on beeches is rather low (Peck, 1989). Beech mast ripens in autumn (September-October), and can be eaten by birds at that time but not during the breeding season, the period most nutritionally demanding. In any case, feeding does not seem to be responsible for the significant relationship between proportions of firs and bird parameters, because this relationship was only found in one of the nesting guilds but we are not aware of diet differences between the two nesting guilds.

Two pieces of evidence suggest that nesting might be behind the relationship between proportion of firs and richness or abundance of bird species that do not rely on existing holes for breeding (mostly non-cavity-nesting birds): (i) as mentioned above, the relationship was only found in one of the nesting guilds; and (ii) the relationship was found in the breeding but not the winter season. Specifically, we would suggest that nest-site selection might be the key factor to understand these results. For example, species like the Firecrest, *Regulus ignicapillus*, and the Goldcrest, *Regulus regulus*, prefer conifers for nesting (Elósegui, 1985). Fir twigs and leaves might provide a safer shelter for nests than those of beeches, or it may be dependent upon bird species phenology, with some bird species beginning reproduction in April, when many beech leaves are not yet fully developed and, consequently, do not hide nests efficiently.

Another interesting result of our study was the positive relationship between richness of birds that do not depend on existing holes for breeding and percentage of shrubs during winter. Shrubs were mainly seedlings of firs and beeches. The presence of a well developed shrub layer has been found to positively influence bird species richness in mountain forests, both in spring and winter (Díaz, 2007). In the case of birds that do not depend on existing holes for breeding, the presence of a shrub layer may ameliorate the harshness of winter weather in a mountain forest such as Irati, and may also decrease the risk of predation through bird concealment. Since secondary cavity-nesting birds can use holes as shelters, the existence of a shrub layer is not as critical for them. Nevertheless, we think that this result should be considered with caution, because the relationship between avian richness and percentage of shrubs in winter was only marginally significant after sequential Bonferroni correction (Tab. III) and heavily depended on data from a single forest plot with high avian richness (Fig. 2).

In summary, our results show that a decrease in the presence of fir and shrub vegetation could adversely affect bird communities during the breeding and winter seasons respectively, at least some bird species that do not depend on existing holes for breeding. Given the problems firs are facing in the study area (Camarero *et al.*, 2004; Solla & Camarero, 2006), an appropriate strategy to benefit biodiversity in this forest would be to maintain a healthy fir population while the mixed forest is favoured against monospecific stands of beech.

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APPENDIX

Bird species observed in beech-fir forests.

Mean (SE) number of individuals per census and forest plot (n = 15 plots) and frequency of occurrence (percentage of forest plots where the species was recorded) at different periods of the year are shown for each bird species. For census and plot characteristics see the text. All species were classified as secondary cavity-nesting birds (SCN) or species that do not depend on holes for breeding (NHD)

Species	Nesting guild	Breeding			Winter		
		Mean	(SE)	Frequency	Mean	(SE)	Frequency
<i>Dryocopus martius</i>	NHD	0.03	(0.03)	6.67	0.00	(0.00)	0.00
<i>Troglodytes troglodytes</i>	NHD	0.40	(0.14)	53.33	0.20	(0.10)	26.67
<i>Erithacus rubecula</i>	NHD	0.90	(0.12)	93.33	0.13	(0.09)	13.33
<i>Turdus merula</i>	NHD	0.20	(0.07)	40.00	0.10	(0.07)	13.33
<i>Turdus philomelos</i>	NHD	0.23	(0.11)	26.67	0.00	(0.00)	0.00
<i>Turdus viscivorus</i>	NHD	0.07	(0.05)	13.33	0.47	(0.11)	60.00
<i>Sylvia atricapilla</i>	NHD	0.23	(0.08)	40.00	0.00	(0.00)	0.00
<i>Phylloscopus collybita</i>	NHD	0.03	(0.03)	6.67	0.00	(0.00)	0.00
<i>Regulus regulus</i>	NHD	1.23	(0.30)	73.33	1.30	(0.23)	80.00
<i>Regulus ignicapilla</i>	NHD	1.33	(0.31)	80.00	0.23	(0.14)	26.67
<i>Poecile palustris</i>	SCN	0.23	(0.11)	33.33	0.23	(0.12)	26.67
<i>Lophophanes cristatus</i>	SCN	0.70	(0.22)	53.33	0.40	(0.18)	33.33
<i>Periparus ater</i>	SCN	0.57	(0.12)	66.67	1.10	(0.21)	80.00
<i>Cyanistes caeruleus</i>	SCN	0.07	(0.07)	6.67	0.53	(0.33)	33.33
<i>Parus major</i>	SCN	0.30	(0.11)	40.00	0.27	(0.10)	40.00
<i>Aegithalos caudatus</i>	NHD	0.07	(0.07)	6.67	0.00	(0.00)	0.00
<i>Certhia familiaris</i>	SCN	0.17	(0.08)	26.67	0.10	(0.05)	20.00
<i>Certhia brachydactyla</i>	SCN	0.23	(0.08)	40.00	0.23	(0.11)	26.67
<i>Sitta europaea</i>	SCN	0.17	(0.06)	33.33	0.23	(0.12)	26.67
<i>Garrulus glandarius</i>	NHD	0.13	(0.10)	13.33	0.00	(0.00)	0.00
<i>Corvus corone</i>	NHD	0.00	(0.00)	0.00	0.07	(0.07)	6.67
<i>Fringilla coelebs</i>	NHD	1.97	(0.21)	100.00	1.90	(0.35)	100.00