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VEGETATIONAL VERSUS TOPOGRAPHICAL EFFECTS ON FOREST BIRD COMMUNITIES: A TEST IN THE CANTABRIAN MIXED FOREST ECOREGION (SPAIN)

EFECTOS DE LA VEGETACIÓN Y LA TOPOGRAFÍA SOBRE LAS COMUNIDADES DE PÁJAROS FORESTALES: UN TEST EN LA ECOREGIÓN DE BOSQUE MIXTO CANTÁBRICO (ESPAÑA)

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SUMMARY.—*Vegetational versus topographical effects on forest bird communities: a test in the Cantabrian Mixed Forest Ecoregion (Spain).*

The physiognomy and floristic composition of vegetation shape the structure of bird communities on a local scale. However, the usefulness of these features in identifying suitable areas for birds can be obscured by other factors, such as altitude, climate and regional landscape patterns. This occurs on large spatial scales (e.g. across latitudinal gradients), and also on smaller, regional scales (e.g. mountains). We explored how topography and vegetation affect breeding and wintering bird communities in mountain forests of the Cantabrian Mixed Forest Ecoregion (Spain), an area where many Palaearctic forest birds reach the southwestern boundary of their ranges. The work was carried out on nine extensive semi-natural forests distributed along the northern slopes of the Cantabrian Mountains from near 400 m to 1,300 m a.s.l. Birds were censused in 78 line-transects 500-m long. Ten physiognomic and floristic variables were measured in each transect. The effects of forest variables, altitude and slope orientation on bird richness and abundance were examined with principal component analysis and general linear models. The results support that, at the study scale, the effects of vegetation on bird communities are very scanty and limited to a positive effect of oak stands on bird richness in winter. Altitude was an outstanding predictor of bird distribution, especially in winter, with the lowest-level forests having the highest bird richness and abundance. This pattern differed quantitatively among species with different foraging niches, since trunk gleaner birds were hardly affected by altitude, whereas the numbers of ground searchers decreased severely. The conservation of the Cantabrian bird communities requires the strict protection of the entire altitudinal forest range, and particularly the existing low altitude forests. Likewise, there is an urgent need to conserve all of the extant oak forests at whatever altitude.

Key words: altitude, bird richness, bird abundance, Cantabrian forests, oak cover, woody plant diversity.

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RESUMEN.—*Efectos de la vegetación y la topografía sobre las comunidades de pájaros forestales: un test en la ecorregión de bosque mixto cantábrico (España).*

La fisonomía y composición florística de la vegetación conforman la estructura de las comunidades de aves a escala local. Sin embargo, la utilidad de estos rasgos para identificar áreas apropiadas para las aves puede quedar oscurecida por la acción de otros factores, como la altitud, el clima y la estructura del paisaje a escala regional. Estos factores actúan a grandes escalas espaciales (en gradientes latitudinales), pero también a escalas menores (regiones montañosas). En este trabajo se explora la influencia de la topografía y la vegetación sobre las comunidades de aves nidificantes e invernantes en la "ecoregión de bosque mixto cantábrico" (España), un área donde muchos pájaros forestales paleárticos alcanzan el borde suroeste de su área de distribución. El trabajo se realizó en nueve bosques extensivos semi-naturales localizados en la ladera norte de la cordillera Cantábrica, con alturas comprendidas entre 400 m y 1.300 m. Los pájaros se censaron en 78 transectos lineales de 500 m de longitud, en los que también se estimaron 10 variables de vegetación. Los efectos de ésta, y de la altitud y orientación de la ladera sobre la riqueza y abundancia de pájaros se analizaron mediante el concurso de análisis de componentes principales y modelos generales lineales. Los resultados demuestran que, a la escala del estudio, los efectos de la vegetación sobre las comunidades aviares son muy escasos y limitados a un efecto positivo de las manchas de robles sobre la riqueza invernal. La altitud es un predictor destacado de la distribución aviar, especialmente en invierno, cuando los bosques localizados en las áreas más bajas mantienen las mayores abundancias y riquezas de aves. Este patrón difirió entre pájaros con distintos nichos de forrajeo, ya que las especies que explotan los troncos apenas fueron afectadas por la altitud, mientras que la abundancia de los pájaros que comen en el suelo descendió drásticamente en niveles altos y medios. La conservación de las comunidades de pájaros forestales de las montañas cantábricas exige la protección estricta de todo el gradiente boscoso altitudinal, en especial de los bosques que todavía persisten en las cotas bajas. Así mismo, es urgente la conservación de todos los robledales.

Palabras clave: altitud, bosques cantábricos, cobertura de robles, diversidad de plantas leñosas, riqueza y abundancia de pájaros forestales.

INTRODUCTION

The structure of bird assemblages is commonly related to the physiognomy and floristic traits of vegetation, a relationship that is at the core of theoretical and applied approaches to the study of this group (Wiens, 1989; Morrison *et al.*, 1998). In the case of forest birds, it has been observed that species richness increases with forest age and complexity. Therefore, adequate management of the structure of forest stands is considered to be the most effective action for improving forest habitats for birds (Morrison, 2002; Ausden, 2004). However, the ability of vegetation to shape bird communities varies at different spatial scales (Kotliar and Wiens, 1990). Whereas studies on the way animal assemblages are structured at local scales have supported the relevance of vegetation or landscape patterns, macro-scale approaches highlight the prevalence of climate or historical events (Wiens, 1989; Noss, 1999; Root *et al.*, 2003).

In this paper we explore the role of vegetation and topography as factors in shaping the richness and abundance of forest birds in the Cantabrian Mixed Forests Ecoregion (PA0406; Olson and Dinerstein, 2002), an area of mountain forests located in northwestern Spain, between the Atlantic Ocean and the Cantabrian Mountains (figure 1). The lowlands have been strongly transformed but the highlands retain large patches of semi-natural forests dominated by broadleaved trees (García *et al.*, 2005). These forests, situated immediately north of the Mediterranean region, are of high conservation concern because they are the last southern refuge of many European forest species (Hagemeijer and Blair, 1997). Thus, the area is included in the Spanish Important Bird Areas designed to protect birds (Viada, 1999), and incorporated within the Spanish list of Natura 2000 Sites.

Some of the factors affecting forest bird communities in the Cantabrian Ecoregion have been specifically or partially addressed by several studies (Carrascal and Tellería, 1990; Tellería and Galarza, 1990; Álvarez and Purroy, 1993). However, none have specifically focused on the forest avifauna of the whole area, even though it maintains one of the most diverse forest bird communities in the Iberian Peninsula (Ramírez and Tellería, 2003; González-Taboada *et al.*, 2007). Such knowledge is essential, however, for the efficient design of the management plans sponsored by the EU regulation to improve conservation of the Natura 2000 Network (Article 6 of the 'Habitats' Directive, 92/43/EEC).

We addressed these issues by studying the breeding and wintering bird communities along 78 transects located in nine large natural forests distributed across the Cantabrian Mountains (fig. 1). In particular, we assessed the role of two main environmental features that affect the structure of bird assemblages:

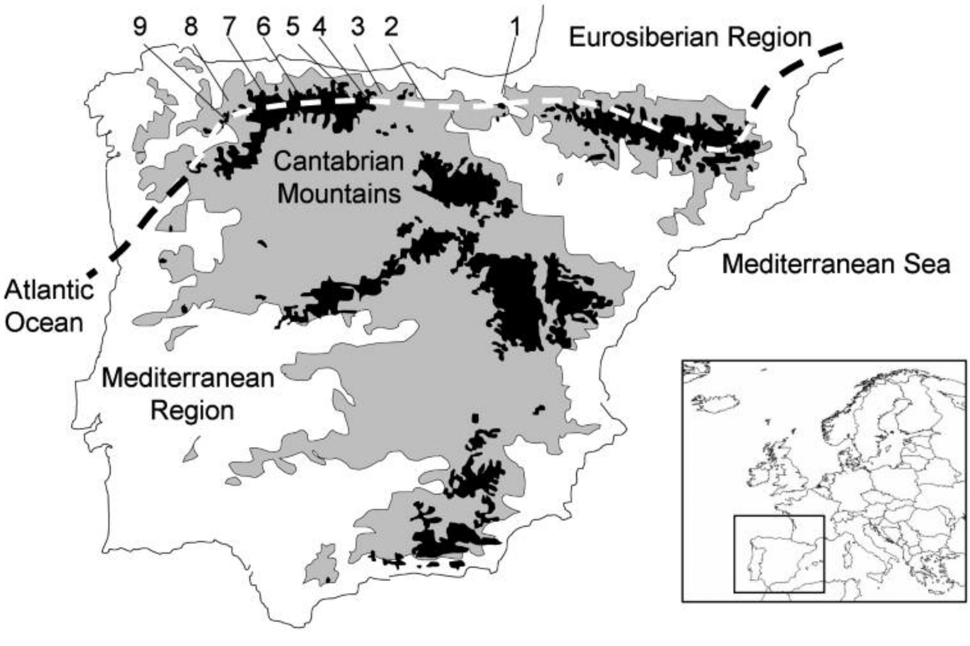

FIG. 1.—Distribution of the studied forests within the Cantabrian Mountains. The dashed line shows the limit between the Eurosiberian and Mediterranean bioclimatic regions. Shadowing indicates elevations above 500 m a.s.l (grey) and above 1,000 m a.s.l. (black). Localities are numbered: 1: Aralar; 2: Altube; 3: Saja; 4: Piedras Luengas; 5: Cosgaya; 6: Tarna; 7: Quirós; 8: Muniellos and 9: Piornedo.
[Distribución de los bosques estudiados en las montañas Cantábricas. La línea de trazos separa las regiones bioclimáticas mediterránea y eurosiberiana. El sombreado gris señala las areas situadas por encima de 500 m de altitud y el negro por encima de 1.000 m. Numeración de las localidades: 1: Aralar; 2: Altube; 3: Saja; 4: Piedras Luengas; 5: Cosgaya; 6: Tarna; 7: Quirós; 8: Muniellos y 9: Piornedo.]

i) *Vegetation*. We explored whether the physiognomic and floristic composition of forests predict the structure of bird communities on a scale of the whole mountain range. Vegetational traits are principal determinants of habitat selection by birds at small, territorial and local scales (Wiens, 1989; Morrison *et al*., 1998), but their influence on a large, regional scale is debated (Kotliar and Wiens, 1990; Luck, 2002). It is thus interesting to know whether vegetational features on the scale of bird territories can predict the structure of bird communities on the scale of the entire Cantabrian Mountains.

ii) *Topography*. We examined the potential role of topographical features in shaping bird assemblages on the scale of Cantabrian Mountain forests. Many species decrease in abundance in areas located at high elevations or on mountain slopes shaded from the sun, a response that is most evident in winter (Huertas and Díaz, 2001; Carrascal and Díaz, 2006). Topography could be thus a factor operating on a regional scale but subject to a seasonal pattern.

METHODS

Study area

We studied nine extensive semi-natural forests distributed along the northern slopes of the Cantabrian Mountains from near 400 m to 1,300 m a.s.l. (table 1, fig. 1). The Cantabrian Mountains have an east/west orientation, intercepting the predominant north-westerly rain fronts arriving from the Atlantic (giving over 1,000 mm of annual precipitation, Ninyerola *et al*., 2005). The northern slopes are thus much wetter than the southern ones, and are dominated by beeches (*Fagus sylvatica*) and Atlantic oaks (*Quercus robur* and *Quercus petraea*), accompanied by a diverse cohort of trees and shrubs (*Betula*, *Salix*, *Corylus*, *Castanea*, *Acer, Ilex, Erica*, *Rubus*, etc.).

TABLE 1

Geographical location (east/west orientation), topography (see fig. 1), sampling effort and tree composition of the studied forests.
[Localización geográfica de este a oeste, topografía, esfuerzo de muestreo y composición del arbolado de los bosques estudiados.]

	Forest locality	**UTM**	**Mean altitude m a.s.l. (min-max)**	**No. of transects**	**Cover of dominant trees (%)**
1	Aralar	30TWN85	888 (753-1,014)	10	*Fagus* (66)
2	Altube	30TWN05	422 (388-476)	6	*Fagus* (43), *Quercus* (27)
3	Saja	30TUN97	740 (551-931)	10	*Fagus* (73)
4	Piedras Luengas	30TUN76	990 (921-1,081)	7	*Fagus* (46), *Quercus* (27)
5	Cosgaya	30TUN57	961 (827-1,021)	10	*Fagus* (27), *Quercus* (18)
6	Tarna	30TUN17	1,188 (1,112-1,265)	5	*Fagus* (60)
7	Quirós	30TTN67	871(586-1,165)	10	*Fagus* (47)
8	Muniellos	29TPH76	1,083 (679-1,302)	12	*Betula* (43), *Quercus* (16)
9	Piornedo	29TPH63	992 (958-1,031)	8	*Quercus* (45)

Bird counts

We delimited 5 to 12 line-transects (500-m long) in each forest (hereafter "localities"), which were censused in June 2005 and January 2006 (N = 78 transects; table 1). We counted all birds seen or heard along each transect. Large-bodied and cryptic species (such as *Accipiter nisus*, *Buteo buteo*, *Strix aluco* or *Caprimulgus europaeus*, all observed in the censuses) cannot be accurately counted by line transects and so they were excluded from the analyses. We initially designed our transects to base our estimates of bird abundance on birds recorded within 50 m of the progression line alone. However, many species occurred at very low density in winter, and consequently were seldom detected within the census belt. Therefore, we finally decided to use all contacts recorded. We are aware that detectability varies among species and such variation is greater outside the census belt. This circumstance should not substantially affect our within-species comparisons (spring *vs* winter abundance) or our analyses of total density when the whole bird community is considered (note that the species composition does not vary substantially between seasons). However, bird detectability may vary between seasons (Bibby *et al.*, 2000), and therefore the latter comparisons should be viewed with care. For example, the detectability of some species may be lower in winter than in spring (as observed for the firecrest *Regulus ignicapillus* and some tit species; L. Mª. Carrascal, *pers. obs.*). In any case, this potential caveat does not affect the most relevant analyses in our study, i.e. the test of the effects of different factors (altitude, vegetation) within seasons.

Passerine and woodpecker species present in at least 10 transects in any season (19 species), were classified according with their dominant use of foraging substrates in winter as (G) ground-searchers, (T) trunk-gleaners, and (F) foliage-gleaners (Carrascal and Tellería, 1985; Carrascal *et al.*, 1987; Carrascal, 1988).

Vegetation structure and topography

We measured the physiognomic and floristic structure of forests by means of two 25-m radius circles distributed at 200 m intervals along each transect. We measured forest physiognomy by visually estimating shrub cover (vegetation under 2-m height), tree cover, tree density (number of trunks with diameter at breast height over 10 cm –see table 3) and tree height. Floristic structure was evaluated by estimating the cover of beeches and oaks, and the number of species of trees (more than 2-m high) and shrubs (less than 2-m high). We averaged the scores of the two sampling circles to characterise each line transect.

We located and measured the altitude (m a.s.l.) of each transect using GPS devices. In addition, we evaluated the mean slope orientation of each transect as the dominant distribution of level curves on 1:50,000 scale maps obtained from the SIGPAC facility (Spanish Ministry of Agriculture, http://www.mapa.es/es/sig/pags/ sigpac/intro.htm). We scored the orientation from 0º (NW) to 180º (SE) around a full range of 360º, since NW orientations are moister and cooler than SE orientations (Marquínez *et al.*, 2003). These scores were cosine-transformed after being recalculated from degrees to radians (Díaz, 2006), thereby obtaining an index that ranged from 1 (cool and rainy NW orientation) to -1 (SE orientation, sunlit at dawn). We used these two topographic features as proxies of climatic harshness (Carrascal and Díaz, 2006).

Statistical analyses

We tested the effects on bird communities of two groups of independent variables, vegetation and topography (altitude and slope

TABLE 2

Abundance (no. individuals/transect ± s.e.) and richness (no. bird species/transect ± s.e.) of bird species in the Cantabrian mountain forests censused during spring and winter (N = 78 transects). The numbers of transects in which each bird species was recorded in spring and winter, respectively, are in parentheses. Results of Wilcoxon matched pairs tests are given for species present in at least 10 transects in any season; bird richness and total abundance are compared with t tests for dependent samples (*: $P \leq 0.05$, **: $P \leq 0.01$, ***: $P \leq 0.001$). [G] ground-searchers, [T] trunk-gleaners, [F] foliage-gleaners.

[Abundancia (nº de individuos/transecto ± e.s.) y riqueza (nº de especies/transecto ± e.s.) de aves en los bosques cantábricos censados en primavera e invierno (N = 78 transectos). En paréntesis, número de transectos en que cada especie fue registrada en primavera e invierno, respectivamente. La abundancia de las especies presentes en al menos 10 transectos en alguna de las dos estaciones se compara entre estaciones con tests de Wilcoxon para muestras apareadas; la riqueza de aves y la abundancia total se comparan mediante tests de la t para muestras dependientes (: $P \leq 0,05$, **: $P \leq 0,01$, ***: $P \leq 0,001$). Gremios tróficos: especies que comen preferentemente en el suelo (G), en el follaje (F) y en los troncos y ramas gruesas (T).]*

	Spring	**Winter**		**Spring**	**Winter**
Columba palumbus (21, 7) $^{\mathrm{ns}}$	0.28 ± 0.05	0.47 ± 0.23	[F] *Regulus ignicapillus* (29, 12)*	0.53 ± 0.09	0.29 ± 0.11
Picus viridis (9, 6)	0.13 ± 0.04	0.08 ± 0.03	[F] *Aegithalos caudatus* (10, 16)$^{\mathrm{ns}}$	0.58 ± 0.21	0.77 ± 0.20
Dryocopus martius (2, 1)	0.03 ± 0.02	0.01 ± 0.01	[T-F] *Poecile palustris* (13, 17)$^{\mathrm{ns}}$	0.32 ± 0.10	0.47 ± 0.12
[T] *Dendrocopos major* (11, 10) $^{\mathrm{ns}}$	0.15 ± 0.04	0.17 ± 0.05	[G-F] *Lophophanes cristatus* (26, 17)*	0.73 ± 0.14	0.36 ± 0.09
Dendrocopos medius (5, 0)	0.08 ± 0.03	–	[F] *Periparus ater* (44, 7)***	1.44 ± 0.19	0.15 ± 0.06
[G] *Troglodytes troglodytes* (60, 13)***	1.94 ± 0.19	0.32 ± 0.10	[F] *Cyanistes caeruleus* (43, 30)**	1.26 ± 0.19	0.67 ± 0.12
[G] *Prunella modularis* (12, 1)**	0.22 ± 0.06	0.03 ± 0.03	[G-F] *Parus major* (38, 19)***	0.91 ± 0.13	0.38 ± 0.09
[G] *Erithacus rubecula* (75, 21)***	3.78 ± 0.22	0.36 ± 0.09	[T] *Sitta europaea* (30, 35)$^{\mathrm{ns}}$	0.81 ± 0.15	0.91 ± 0.15

TABLE 2 (cont.)

	Spring	**Winter**		**Spring**	**Winter**
[G] *Turdus merula* (57, 21)***	1.55 ± 0.16	0.60 ± 0.15	*Certhia familiaris* (3, 5)	0.05 ± 0.03	0.08 ± 0.04
[G] *Turdus philomelos* (54, 6)***	1.29 ± 0.14	0.09 ± 0.04	[T] *Certhia brachydactyla* (28, 19)^{ns}	0.60 ± 0.11	0.35 ± 0.08
Turdus iliacus (–, 5)	–	0.54 ± 0.29	*Garrulus glandarius* (24, 27)^{ns}	0.38 ± 0.07	0.68 ± 0.13
Turdus viscivorus (8, 8)	0.14 ± 0.05	0.18 ± 0.07	[G-F] *Fringilla coelebs* (67, 8)***	3.04 ± 0.27	0.13 ± 0.05
Sylvia borin (18, –)	0.29 ± 0.07	–	[G] *Serinus serinus* (11, 0)**	0.14 ± 0.04	–
[F] *Sylvia atricapilla* (70, 1)***	3.14 ± 0.26	0.01 ± 0.01	*Carduelis carduelis* (0, 1)	–	0.01 ± 0.01
Phylloscopus bonelli (4, –)	0.09 ± 0.05	–	*Carduelis spinus* (0, 1)	–	0.01 ± 0.01
[G] *Phylloscopus collybita/ibericus* † (19, 1)***	0.32 ± 0.07	0.01 ± 0.01	*Pyrrhula pyrrhula* (9, 6)	0.18 ± 0.06	0.27 ± 0.14
Regulus regulus (4, 1)	0.05 ± 0.02	0.01 ± 0.01	*Emberiza cia* (4, 1)	0.05 ± 0.03	0.01 ± 0.01
Mean bird richness***	10.4 ± 0.299	4.1 ± 0.374			
Mean abundance***	24.5 ± 0.895	8.4 ± 0.968			

† *P. ibericus* is present exclusively as breeder.

orientation), while controlled for the spatial autocorrelation with a second degree Legendre's polynomial (Borcard *et al.*, 1992); so, we included five spatial covariates derived from the geographical coordinates of every transect. We conducted a Principal Component Analysis on the physiognomic and floristic features of vegetation (10 variables), to reduce the number of variables. We then used the factor scores of the selected components to probe the effects of forest structure and physionomy. We thus included geographical covariates, altitude, slope orientation and the PC vegetation traits as covariates in general linear models (GLM; StatSoft, 2002).

We applied similar analyses to the most abundant passerine species, those present in at least 16 transects out of 78 census transects (20%). These analyses were used to explore whether the effects of vegetation and topography on the distribution of individual species were similar to the observed patterns on a community scale. We tackled the problem of multiple statistical tests by lowering the α values to 0.01, and by reporting exact p-values (see Moran, 2003).

RESULTS

Three of the 34 species recorded were summer visitors (garden warbler *Sylvia borin*, and Iberian and Bonelli's warblers *Phylloscopus ibericus* and *P. bonelli*) and the redwing *Turdus iliacus* was the only strictly migratory species detected in winter (table 2); the Iberian warbler and the chiffchaff *Phylloscopus collybita* were analyzed together since they can not always be identified with certainty –see Cuesta and Balmori, 2003). Despite this seasonal constancy in species-composition, the arrival of winter was associated with major changes in the structure of the bird communities (table 2). Total abundance and species richness per transect severely decreased from spring to winter (t-test for dependent samples, N = 78 transects, abundance: t = 15.894, $P < 0.001$; richness: t = 15.998, $P < 0.001$); in short, bird communities lost 60% of their species and and 66% of their individuals in winter (table 2). Abundance and species richness per transect were strongly correlated (Pearson correlation coefficient, spring: $r_{78} = 0.75$, $P < 0.001$; winter: $r_{78} = 0.88$, $P < 0.001$), supporting the view that species richness was the main determinant of abundance at the scale of 0.5 Km transect units.

Fourteen out of 19 widespread species of passerines and woodpeckers decreased their abundance in winter, and five did not show

TABLE 3

Results of the PCA carried out on floristic and physiognomic variables (1-4 and 5-10, respectively) measured on transects. Factor loadings of variables, eigenvalues and variance explained by each component are given.
[Resultados del análisis de componentes principales realizado sobre las variables fisionómicas (las cuatro primeras) y florísticas (las seis últimas) medidas en los transectos. Se exponen los números-peso de las variables, los eigen-valores y la varianza explicada por cada componente.]

	PC1	PC2	PC3
Shrub species	0.839	–0.201	–0.257
Tree species	0.712	–0.326	–0.225
Oak cover	0.488	0.229	0.758
Beech cover	–0.727	–0.462	–0.219
Shrub cover	0.837	0.266	–0.193
Tree cover	–0.013	–0.818	0.234
Tree height	–0.836	0.096	0.187
Trunks 10-30 cm	0.612	–0.468	0.454
Trunks 30-50 cm	–0.485	–0.427	–0.040
Trunks > 50 cm	–0.878	0.137	0.148
Eigenvalue	4.76	1.58	1.10
Variance (%)	47.6	15.8	11.0

significant differences between seasons. The first group included six ground searchers, five foliage gleaners, and three mixed, foliage-ground foragers, whereas trunk gleaners were dominant in the second one (table 2).

Factors affecting bird communities

Principal component analyses (PCA) on vegetation data defined three gradients that accounted for 74.4% of variance (table 3). The first component (PC1) was a combination of physiognomic and floristic traits opposing stands covered by dense shrubs and with increasing values of tree and shrub richness to the developed stands dominated by tall and thick beeches. The second component (PC2) defined a gradient of increasing tree cover, and the third (PC3) a gradient of increasing oak cover. PC1 kept a rough change with altitude, since shrub and tree diversity increases with altitude in the study area, whereas the traits associated with developed woodland

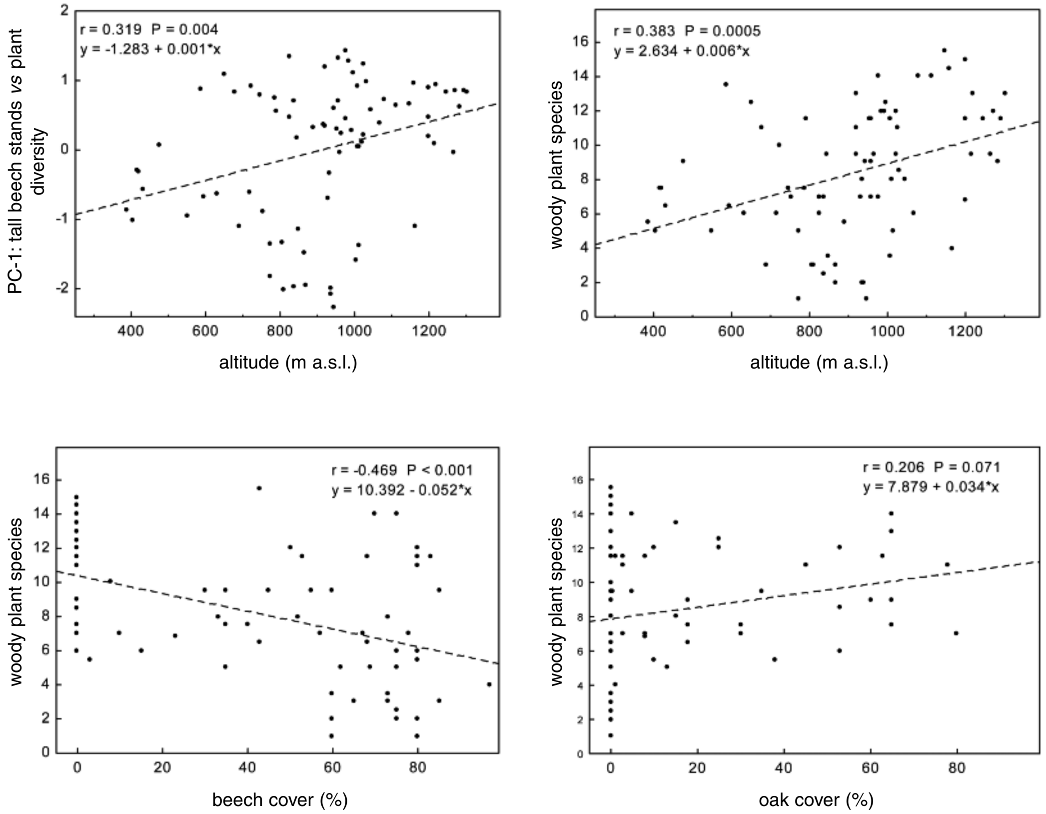

FIG. 2.—Relationships between altitude and principal component PC1 and number of tree and shrub species (top), and oak and beech cover with the number of tree and shrub species (bottom).
[Arriba: Relaciones de la altitud con el componente principal PC1 (izquierda) y con el número de especies de árboles y arbustos (derecha). Debajo: Relaciones de la cobertura de hayas (izquierda) y robles (derecha) con el número de especies de árboles y arbustos.]

show the opposite trend (fig. 2). Another conspicuous feature is the mutually exclusive distribution of beech and oak woodlands ($r_{78} = -0.58$, $P < 0.001$), and the positive tendency of oak cover to be associated with tree and shrub diversity, contrasting with the reverse pattern for beech (fig. 2).

The four GLMs carried out on the structure of bird assemblages reported significant decreases of bird richness and abundance with altitude (table 4). The effects were particularly strong in winter, when models explained over 50% of variance. In contrast, the influence of vegetation was scarce and limited to a positive effect of oak cover (PC3) on bird richness in winter (table 4 and fig. 3).

Factors affecting the abundance of individual species

After of controlling for spatial autocorrelation, 15 out of 23 species models related to any vegetation or topographic trait, and 13 of them were significant (explained variance: 23.4% to 58.2%, mean: 39.4%; see appendix). Effects of vegetation or topography covariates ≤ 0.01 were recorded in 11 models (in fact, all were < 0.002; appendix); altitude entered in 9 of these models, always with negative effects (appendix; fig. 4). Other three covariates entered in one model in spring (fig. 4): so, the robin *Erithacus rubecula* showed preference for cool-shaded slopes (slope

TABLE 4

Results of the general linear models (GLM) carried out on species richness and abundance of forest birds. Covariates: altitude, orientation, physiognomic and floristic traits of forests (PC1, PC2 and PC3), and five geographical covariates (significant F values are given with their sign).
[Resultados de los modelos generales lineales realizados con la abundancia y riqueza de aves forestales. Covariantes: altitud, orientación, estructura y composición florística de los bosques (PC1, PC2 and PC3) y cinco variables de posición geográfica; sólo se dan las F (con su signo) de las covariantes con efectos significativos.]

		Spring richness			**Winter richness**		
	d.f.	**r²**	**F**	**P**	**r²**	**F**	**P**
Altitude	1, 67		–8.437	0.005		–53.588	<<0.001
PC3 (oak cover)	1. 67					+3.958	0.051
Whole model	10, 67	24.0	2.116	0.035	55.1	8.217	<<0.001

		Spring abundance[1]			**Winter abundance**[2]		
	d.f.	**r²**	**F**	**P**	**r²**	**F**	**P**
Altitude	1, 67		–13.948	0.0004		–43.977	<<0.001
Whole model	10, 67	36.7	3.886	0.0003	49.2	6.494	<<0.001

[1] significant effects of 4 geographical covariates.

[2] idem of 3 geographical covariates.

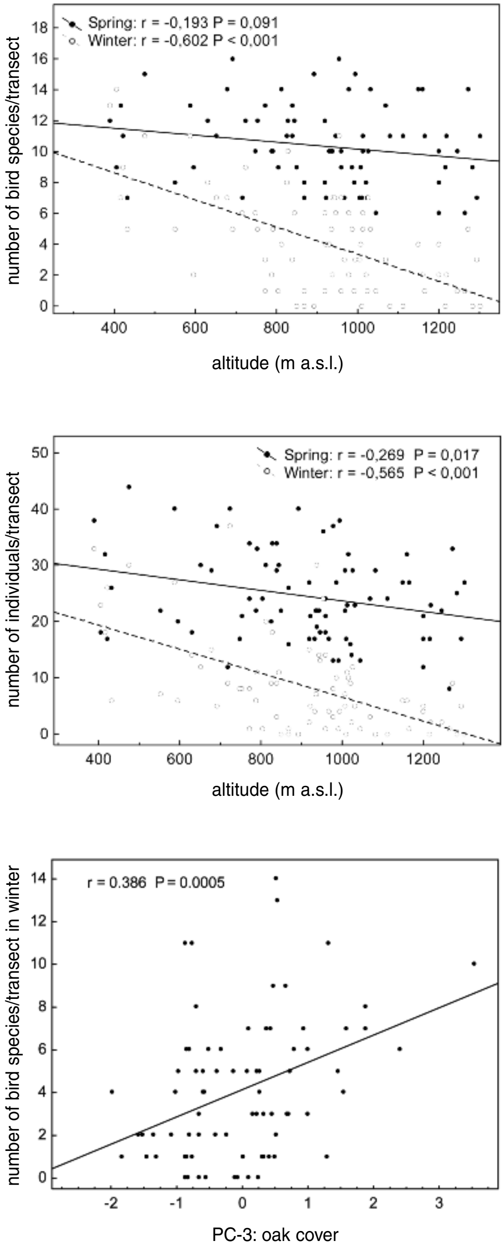

FIG. 3.—Main relationships between the independent variables of the GLMs carried out and the abundance and richness of bird assemblages (table 4).

[Relaciones significativas entre las covariantes usadas en los GLMs y la abundacia y riqueza de las comunidades de aves (véase la tabla 4).]

orientation), the numbers of the blackcap *Sylvia atricapilla* increased with the diversity of woody plants (PC1), and oak cover (PC3) positively influenced the abundance of the chaffinch *Fringilla coelebs*.

DISCUSSION

Our results show that a single topographic factor, namely altitude, accounted for most variation found in avian distribution patterns, both at the community and species level, whereas vegetation seemingly had a negligible role. We here discuss the effects of these factors and conclude by drawing some conclusions applicable to the conservation of the Cantabrian forest bird communities.

Effect of altitude on bird communities

Altitude extensively affected the bird communities of Cantabrian forests, especially in winter, when both richness and abundance suffered dramatic losses at high elevations (fig. 3). Altitude had significant negative effects in all community models ($P \leq 0.005$; table 4), and in 9 out of 23 individual ones ($P \leq 0.002$; appendix); in 8 out of these 9, altitude was the only factor with significant effects. Our results thus support the strong regional role of topography in the organization of the Cantabrian avifauna. These results fit the expected pattern, since the study area extended across an altitudinal gradient 1,000 m broad, and since loss of richness with altitude is a common regional pattern at temperate latitudes (Begon *et al.*, 2006; Lomolino *et al.*, 2006), which has been detected for birds in many European mountain ranges (e.g., Álvarez and Purroy, 1993; Carrascal *et al.*, 2002; Díaz, 2006; Archaux and Bakkaus, 2007).

The loss of species with altitude has been associated with the effects of climatic harshness in mountains, including drastic decreases of productivity and food availability, particu-

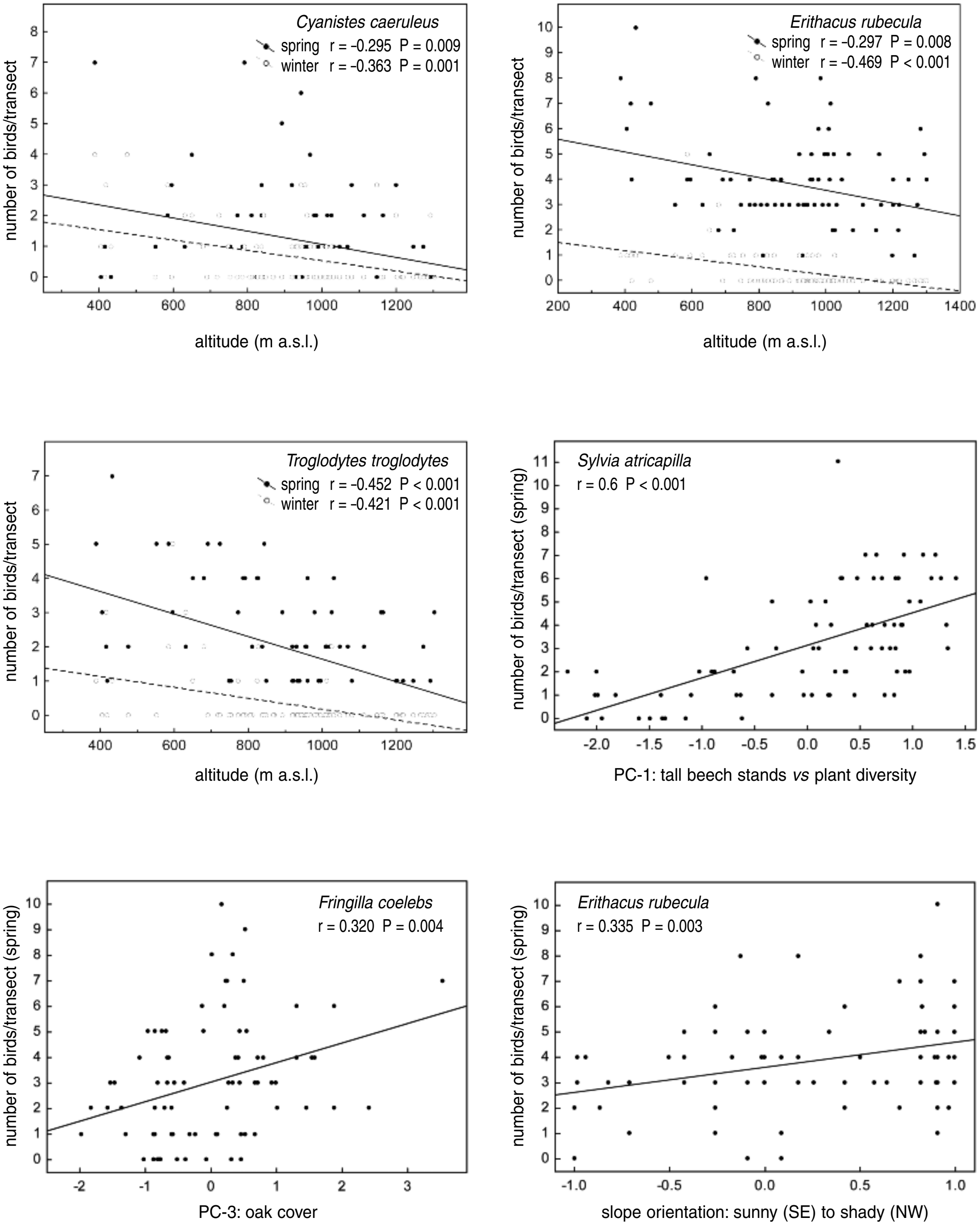

FIG. 4.—Representative relationships between the independent variables of the GLMs carried out and the spring or winter abundances of individual bird species (see appendix).

[Muestra representativa de las relaciones entre las covariantes usadas en los GLMs y la abundancia primaveral o invernal de las especies analizadas (véase el apéndice).]

larly in winter (Begon *et al.*, 2006). In compliance with other studies carried out in particular sectors of the the Cantabrian range (Tellería and Galarza, 1990; Álvarez and Purroy, 1993), and in other Iberian mountains (Carrascal *et al*, 1987; Carrascal, 1988), the effects of altitude were more striking for foliage gleaners and especially for ground searchers, two foraging guilds particularly vulnerable to food shortages related to frosts and snowfalls at highland sites, so that they are likely to be driven to lower (and warmer) forest patches during winter. For example, ground searchers totally abandons high elevations of central Spain during snowstorms (Carrascal, 1988; see also Carrascal *et al.*, 1987). In this context, it is relevant to point out that four species of ground searchers (the wren *Troglodytes troglodytes*, the robin, the blackbird *Turdus merula*, and the songthrush *Turdus philomelos*) accounted for the 45% of the decrease in winter abundance in our area. However, trunk gleaners mainly rely on trunk and branch invertebrates, whose availability is only moderately affected by winter weather (Carrascal, 1988). Hence, species in this guild experience less restrictive trophic conditions and their foraging substrata, in the core of the trees, are more sheltered from inclement weather than peripheral substrata (Carrascal, 1988).

Effects of vegetational structure on bird communities

The complexity of vegetational structure and floristic diversity are the commonest factors explaining the richness of bird communities, basically through their effects on niche diversification (MacArthur and MacArthur, 1961; Wiens, 1989). Many studies carried out on an intermediate regional scale have thus shown that diversity of woody plants and structural complexity of vegetation improve the richness of breeding forest birds (Díaz, 2006; Archaux and Bakkaus, 2007; Gil-Tena *et al.*, 2007). In contrast, our results imply a very weak role of vegetation as a predictor of bird richness and abundance on the scale of the Cantabrian Mixed Forest Ecoregion, and also when vegetational effects were examined at the species level. It must be pointed out, however, that the nine studied forests extend east/west for 440 km and from 390 to 1,300 m a.s.l. It may therefore be expected that the role of vegetation will be lessened by factors acting on broader temporal and spatial scales, such as climatic, geographical and historical effects (Ramírez and Tellería, 2003, Carrascal and Lobo, 2003; González-Taboada *et al.*, 2007).

Another aspect to be considered is that the main vegetational features favouring bird richness and abundance are somewhat concentrated at opposite ends of the altitudinal gradient. Thus, while well developed but scarcely diversified woodlands are rather dominant at low and mean altitudes, the greatest values of floristic diversity are associated with forest stands chiefly located at higher levels (PC1 vegetation gradient). Hence, this pattern could prevent the existence of relevant effects of plant diversity on bird communities, above all in winter, since at this season high altitude has very great negative effects on most bird species (fig. 3). The sole floristic, although rather weak effect, was that of oak-dominated stands (PC3) on bird richness in winter (table 4). In fact, oak cover was the only factor that counteracted the strong negative effect of altitude in any community model; likewise, oak cover positively affected the abundance of the chaffinch in spring. These results are rather similar to those revealed by more local studies that show the importance of oak trees for forest birds in the east of Cantabrian range, in particular for trunk and foliage gleaners in winter (Carrascal and Tellería, 1985, 1989).

Management implications

From a conservation perspective, our results support the view that, at our study scale, the distribution of forest bird assemblages in the Cantabrian Mixed Forest Ecoregion is mostly related to the critical influence of altitude, whereas the other factors checked have a rather secondary importance. This is an expected result given the latitudinal position of the Cantabrian Ecoregion, and that our transects were conducted from 390 to 1,300 m a.s.l., an altitudinal belt thoroughly representative of the vertical distribution of Cantabrian forests. In fact, the four richness and abundance community parameters significantly match a gradient of altitude (fig. 3). It may thus be concluded that altitude constitutes a good predictor of forest suitability for the whole forest bird community within a wide range of vegetation conditions. The relevance of altitude is reinforced by the fact that large numbers of wintering birds probably originate from breeding populations that move to lower elevations for the winter (Álvarez and Purroy, 1993; Tellería *et al.*, 1999, 2001). Therefore, the conservation of Cantabrian forest birds requires the strict protection of the entire altitudinal forest range, and particularly the existing low altitude forests, which are doubtless the most threatened by urban and industrial development (García *et al.*, 2005). Unfortunately, lowland forests have historically been destroyed by agricultural and urban encroachments in the Cantabrian area (García *et al.*, 2005), and the remaining ones are mostly managed for commercial forestry, involving measures that reduce woody plant diversity, a trait which seemingly benefit bird richness at local scales. Likewise, it is urgent to conserve all of the extant oak forests at whatever altitude, given the importance of these natural stands in the maintenance of bird richness during winter, and their history of retreat resulting from the continuous spread of beech (Rozas, 2001).

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APPENDIX 1 *[APÉNDICE 1]*

Results of the general linear models (GLM) carried out for abundance of species present on at least 16 transects (see table 2 for full names) as a function of vegetational (PC1, PC2, and PC3) and topographical (altitude and orientation) traits, controlling by spatial autocorrelation (five geographical covariates). The number of transects on which each species was recorded is given in parentheses. Significant F values are given with their sign (d.f.: 1, 67 for fixed variables; bold type: covariate effects ≤ 0.010). Species that did not correlate with any trait: *R. ignicapillus* spring ($r^2 = 9.7$, F = 0.720, P = 0.703, N = 29 transects), *S. europaea* spring ($r^2 = 18.1$, F = 1.480, P = 0.166, N = 30), *P. ater* spring ($r^2 = 31.4$, F = 3.064, P = 0.003, N = 44), *L. cristatus* spring ($r^2 = 41.0$, F = 4.655 , P = 0.00005, N = 26), *P. major* spring ($r^2 = 16.4$, F = 1.314, P = 0.241, N = 38), *S. borin* spring ($r^2 = 24.6$, F = 2.191, P = 0.029, N = 18), *L. cristatus* winter ($r^2 = 19.7$, F = 1.640, P = 0.114, N = 17), *P. palustris* winter ($r^2 = 14.6$, F = 1.141, P = 0.346, N = 17).

[Resultados de los modelos generales lineales realizados con la abundancia de las especies registradas en al menos 16 transectos (nombres completos en la tabla 2) en función de los rasgos de vegetación (PC1, PC2 y PC3) y topografía (altitud y orientación), controlados por autocorrelación espacial (5 covariantes geográficas). En paréntesis, número de transectos en que cada especie fue registrada. Se exponen los valores de las F (con su signo) de las covariantes con efectos significativos (aquellos con P ≤ 0,010 se señalan en negrita); grados de libertad = 1, 67 para las covariantes y 10, 67 para los modelos. Especies que no se correlacionan con ningún rasgo: R. ignicapillus *primavera ($r^2 = 9,7$, F = 0,720, P = 0,703, N = 29 transectos),* S. europaea *primavera ($r^2 = 18,1$, F = 1,480, P = 0,166, N = 30),* P. ater *primavera ($r^2 = 31,4$, F = 3,064, P = 0,003, N = 44),* L. cristatus *primavera ($r^2 = 41,0$, F = 4,655, P = 0,00005, N = 26),* P. major *primavera ($r^2 = 16,4$, F = 1,314, P = 0,241, N = 38),* S. borin *primavera ($r^2 = 24,6$, F = 2,191, P = 0,029, N = 18),* L. cristatus *invierno ($r^2 = 19,7$, F = 1,640, P = 0,114, N = 17),* P. palustris *invierno ($r^2 = 14,6$, F = 1,141, P = 0,346, N = 17).]*

Spring	**PC1 plant diversity**	**PC2 forest cover**	**PC3 oak cover**	**altitude**	**slope**	**whole model (g.l. = 10, 67)**		
						r^2	**F**	**P**
E. rubecula (75)				-10.758 **0.002**	+12.816 **0.0006**	33.9	3.429	0.001
F. coelebs (67)			+10.278 **0.002**	+4.2452 0. 043		51.2	7.021	2.0^{-7}
S. atricapilla (70)	+10.001 **0.002**	-6.546 0.013				58.2	9.311	2.0^{-9}
T. troglodytes (60)				-37.243 **1.0^{-7}**		48.3	6.268	1.0^{-6}
T. merula (57)				-4.201* 0.044		23.4	2.042	0.042
T. philomelos (54)	-5.113 0.027					11.5	0.869	0.567
C. brachydactyla (28)	-5.457 0.022			-12.528 **0. 0007**		51.0	6.977	2.0^{-7}
C. caeruleus (43)				-10.953 **0. 002**		24.4	2.163	0.031

APPENDIX 1 *[APÉNDICE 1]* (cont.)

Winter	**PC1 plant diversity**	**PC2 forest cover**	**PC3 oak cover**	**altitude**	**slope**	**whole model (g.l. = 10, 67)**		
						r^2	**F**	**P**
E. rubecula (21)				–40.033 **2.0^{-8}**		44.0	5.256	1.0^{-5}
T. merula (21)				–46.289 **3.0^{-9}**		49.1	6.453	1.0^{-6}
A. caudatus (16)				–10.201 **0.002**		18.8	1.554	0.140
C. brachydactyla (19)					+4.124 0. 046	43.5	5.149	2.0^{-5}
C. caeruleus (30)				–23.334 **8.0^{-6}**		32.2	3.187	0.002
P. major (19)			+5.020 0.028			19.5	1.620	0.120
S. europaea (35)				–7.163 **0.009**		29.3	2.774	0.006