

BIRD-HABITAT RELATIONSHIPS IN A VEGETATIONAL GRADIENT IN THE ANDES OF CENTRAL CHILE¹

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Abstract. An unusual pattern has been described in Patagonian forests, where bird species diversity seems to be inversely correlated with vegetation complexity. To test the occurrence of this pattern in the northern *Nothofagus* forests of central Chile, a study was conducted at the Ñuble National Reserve during the austral summers of 1994 and 1995. Twenty-nine plots were set along a vegetational gradient. In each plot, the density of all diurnal bird species was estimated, and the vegetation composition and structure were measured. The highest and the lowest bird species diversity were found in semideciduous scrub habitat and Poaceae steppes, respectively. In nongrassland sites, no vegetation variable explained bird species richness or diversity. Total foliage volume and foliage height diversity were significantly correlated with bird species diversity in the nonforest sites but not in the forested areas. However, foliage height diversity significantly explained the variation of bird density and bird species richness in the forest sites. The presence of the tree *Nothofagus obliqua* was positively correlated with bird diversity and insectivore density. The patterns observed at Ñuble lie between the traditional positive relationship between bird diversity and foliage diversity and the inverse relationship found in Patagonia. I propose that particular floristic features of the vegetation rather than structure itself might explain better the diversity of bird species in Patagonian forests.

Key words: *bird communities, Chile, Patagonian forests, diversity, vegetation structure, Nothofagus.*

INTRODUCTION

Temperate forest birds have been poorly studied in Chile, and few investigations have described the composition and structure of entire bird communities (Jaksic and Feinsinger 1991). Moreover, all these studies have been conducted in evergreen or semideciduous lowland forests, leaving the bird assemblages of the deciduous beech forests in the Andes cordillera of central and southern Chile virtually unknown. Vuilleumier (1972) described an unexpected pattern in bird communities in northern Patagonia in Argentina. He found fewer species in beech forests than in the structurally simpler scrub-steppe habitats. In the same area, Ralph (1985) found a significant inverse relationship between foliage complexity and bird diversity in nongrassland sites.

The aim of the present study is to describe habitat associations of bird communities in a forest-scrub-steppe gradient in the Andes of central Chile and to determine whether they exhibit the patterns found by Ralph (1985).

METHODS

The study was conducted at the Ñuble National Reserve in central Chile (Fig. 1). This area includes two ecological subregions: "Bosque Caducifolio Montano" and "Cordilleras de la Araucanía" (Gajardo 1994). Most of the 720 km² Reserve is covered with upland steppes of *Festuca* and *Chusquea*, deciduous scrub of *Nothofagus antarctica* or *N. pumilio*, and deciduous forests of *N. obliqua* and *N. pumilio* (Faúndez et al. 1994). Mean annual precipitation within the Reserve ranges from 2.3 to 3.3 m; mean minimum temperature in July ranges from -1.2°C to 0.9°C; and mean maximum temperature in January ranges from 14.8°C to 22.1°C (Santibáñez and Uribe 1993).

Bird censuses were carried out during February 1994 and January 1995, corresponding to the late breeding season. Twenty-nine census sites were established along a vegetational gradient from steppe to forest. When possible (20 sites), variable line transects (Burnham et al. 1980) were used to estimate bird density. At sites where walking was difficult (nine sites) variable circular plots were used (Buckland 1987). I assumed that these two methods produced similar estimates of a population's density (Ralph 1985). Observations were carried out be-

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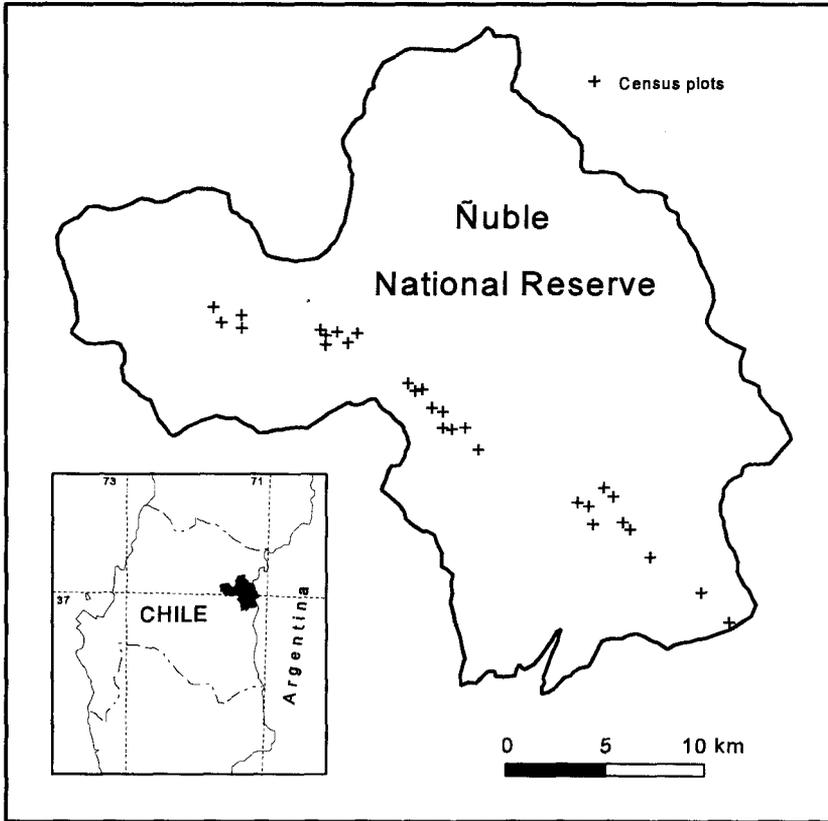


FIGURE 1. Geographic location of the study area, Ñuble National Reserve, in central Chile.

tween 08:00 and 12:00. Detections were recorded at intervals of 10 m, with a maximum detection distance of 80 m. Flying birds were not recorded unless they showed clear evidence of using the plot (e.g., swallows hunting insects). Censuses were conducted by two observers, each contributing roughly 50% of the observations within each plot. Transects or points were surveyed 4–10 times in 1994 and 6 times in 1995. Data for each bird species at each census site were pooled to estimate population density. Densities from 1994 and 1995 were averaged and their variances were calculated.

Bird species diversity (BSD) at each site was calculated using the Shannon-Wiener (H') diversity index (MacArthur and MacArthur 1961). Bird species richness (BSR) at each site was estimated using the jackknife procedure (Heltshe and Forrester 1983). To eliminate the effect of sample size, richness estimates were corrected using a logarithmic transformation and were

standardized as the number of species on a 2-ha area.

At every site, foliage structure and plant species composition were described in four horizontal layers (0–0.2, 0.21–2, 2.1–8, and 8.1–16 m). In each layer, total foliage volume (TFV_{layer}) was estimated as the proportion of the layer occupied by plant leaves, twigs, and branches. This proportion was multiplied by the layer's height to obtain its TFV_{layer} (m^3 per 0.01 ha). The relative species frequency at each layer was multiplied by the TFV_{layer} to obtain foliage volume for individual species. The site's total foliage volume (TFV) and individual species' foliage volume were calculated by the addition of the four TFV_{layer} values. Vegetation measures were estimated in both 1994 and 1995 and then averaged. Plant species diversity (PSD) was estimated for each layer and for the entire site using the proportion of the TFV_{layer} and the proportion of the TFV represented by all the species, re-

spectively. With these values, an H' index of diversity was calculated. In order to determine an index of foliage height diversity (FHD), the three upper layers were divided into two equal sub-layers whose TFV_{layer} were calculated. This subdivision was done because the four original layers were considered inappropriate to describe the foliage profile precisely. Finally, the TFV_{layer}/TFV ratios for the seven resulting layers were used to estimate the H' index.

As a way of identifying different kinds of habitats for birds, the census sites were grouped initially in terms of their vegetation structure and composition using hierarchical clustering (Digby and Kempton 1987). However, to make the resulting classification more consistent with field observations of bird assemblages, two sites were arbitrarily reassigned to another type of habitat. Finally, nine vegetation types (bird habitats) were recognized at the studied area. These are:

1. *Nothofagus pumilio* forest (NpF). High-elevation (1,300–1,700 m) deciduous beech forest, on wind-protected slopes. Trees 10–14 m tall. Sparse understory (two sites).

2. *N. obliqua* forest (NoF). Low-elevation (1,000–1,200 m) deciduous beech forest, located in protected valleys and slopes. Trees 8–12 m tall. Sparse to dense understory (six sites).

3. *N. obliqua-pumilio* forest (NopF). Mid-elevation (1,200–1,400 m) highly stratified deciduous beech forest. Located mainly on south-facing slopes in protected valleys. Dense understory of *Chusquea argentina*. Trees 14–16 m tall (five sites).

4. *Austrocedrus chilensis-N. obliqua* forest (AcNoF). Low-elevation (1,000–1,200 m) mixed cedar-beech forest. Occurs on rocky slopes. Very sparse overstory and understory. Trees 8–12 m tall (one site).

5. Semideciduous scrub (SS). Low-elevation (1,000–1,200 m) scrub. Located on dry slopes. Composed mainly of *Colletia hystrix*, *C. argentina*, *Diostea juncea*, and *Fabiana imbricata*, with a few scattered beech trees. Scrub 0.5–4 m tall (three sites).

6. *N. antarctica* low scrub (NaLS). High-elevation (1,600–2,000 m) deciduous scrub. Located in very windy and cold zones. On some sites *N. antarctica* is replaced by *N. pumilio* but this does not alter the overall structure of the habitat. Scrub 0.5–1.5 m tall (two sites).

7. *N. antarctica* tall scrub (NatS). Mid-ele-

vation (1,200–1,400 m) deciduous scrub. In open valley bottoms. Sparse scrub with dense grass (mainly *Festuca*) cover. Scrub 2–5 m tall (five sites).

8. *Chusquea argentina* steppe (CaS). Mid-to high-elevation (1,300–1,900 m) steppe. Occurs in many topographic situations. Composed mainly of *C. argentina* and *Festuca scabriuscula*. Lower than 0.5 m tall (three sites).

9. Poaceae steppe (PS). Mid to high-elevation (1,300–2,000 m) steppe. Located in windy zones. Main species are grasses of the genus *Agrostis*, *Festuca*, *Poa*, and *Hordeum*. In some zones there is a sparse shrub cover of mainly *Chilotrimum rosmarinifolia* (two sites).

The use of these habitats by bird species was described in terms of their mean absolute densities. A measure of habitat breadth (B) was calculated for all species using the relation $B(x) = e^{2p_i \log(p_i)}$, used by MacArthur (1964), where p_i is the density of species x in habitat i divided by the sum of densities for the species at all the habitats studied. Birds were assigned to trophic guilds following Johnson (1967) and Jaksic and Feinsinger (1991) and using the author's field experience. Bird species names follow Araya and Chester (1993), and plant names follow Marticorena and Quezada (1985).

Linear regression analysis and Pearson correlations were performed in order to relate birds with vegetation variables and individual plant species. For this last analysis, only species (plants and birds) recorded at five or more sites were considered.

RESULTS

BIRDS

Forty-six bird species were recorded during the transect and point surveys (Table 1). The most abundant species were the White-crested Elaenia (1.37 ha⁻¹), Black-chinned Siskin (1.30 ha⁻¹), Thorn-tailed Rayadito (0.86 ha⁻¹), Common Diuca-Finch (0.78 ha⁻¹), and House Wren (0.77 ha⁻¹). Another 22 species were recorded on the sites but not on official counts (Table 1). The latter species were very uncommon in the reserve and were normally observed only once or twice during the entire study.

Bird communities showed important differences among habitats (Table 1). Estimated mean density of all birds ranged from 3.36 ha⁻¹ in Poaceae steppe to 20.64 ha⁻¹ in *N. obliqua-pumilio*

TABLE 1. Continued.

Species	Diet*	Sub- strate**	Mean bird density (ha ⁻¹) in indicated habitats:										Habitat breadth (β)	
			NpF***	NoF	NopF	AcNoF	SS	NaIS	NaTS	CaS	PS			
Andean Tapaculo (<i>Scytalopus magellanicus</i>)	I(G)	G(F)	0.67	0.23	1.41	0.09	0.05	—	—	1.32	0.29	—	—	5.68
Great Shrike-Tyrant (<i>Agriornis livida</i>)	I	F(A)	—	—	—	—	—	—	—	+	—	—	—	—
Black-billed Shrike-Tyrant (<i>Agriornis montana</i>)	I	F(A)	—	—	—	—	—	—	—	—	—	—	—	1.00
Tufted Tit-Tyrant (<i>Anairetes parulus</i>)	I(F)	F	+	0.15	0.17	+	0.31	—	0.02	—	—	—	—	2.96
Patagonian Tyrant (<i>Colorhamphus parvirostris</i>)	I	F(A)	+	—	0.50	—	—	—	—	0.07	—	—	—	1.66
White-crested Elaenia (<i>Elaenia albiceps</i>)	I(F)	F(A)	2.68	3.62	4.03	0.17	1.64	0.45	—	0.63	0.84	—	—	6.47
Rufous-backed Negrilo (<i>Lessonia rufa</i>)	I	G	—	—	—	—	—	—	—	0.02	—	—	0.13	1.64
Plain-capped Ground-Tyrant (<i>Muscisaxicola alpina</i>)	I	G	0.03	—	—	—	—	0.04	—	—	—	—	—	1.43
White-browed Ground-Tyrant (<i>Muscisaxicola albilora</i>)	I	G	—	—	—	—	—	+	—	—	—	—	—	—
Rufous-naped Ground-Tyrant (<i>Muscisaxicola rufivertex</i>)	I	G	—	—	—	—	—	+	—	—	—	—	—	—
Spot-billed Ground-Tyrant (<i>Muscisaxicola maculirostris</i>)	I	G	—	—	—	—	—	—	—	—	—	—	—	—
Fire-eyed Djucon (<i>Pyrope pyrope</i>)	I(F)	A	0.26	0.28	0.07	—	0.11	—	—	0.14	—	—	+	3.72
Rufous-tailed Plancutter (<i>Phytotoma rara</i>)	H(F)	F	0.04	0.29	—	—	0.11	—	—	0.03	—	—	—	3.12
Chilean Swallow (<i>Tachycineta leucopyga</i>)	I	A	+	+	0.06	—	+	+	—	—	—	—	—	1.00
Blue-and-white Swallow (<i>Pygochelidon cyanoleuca</i>)	I	A	+	+	—	—	+	+	—	—	+	—	—	—
House Wren (<i>Troglodytes aedon</i>)	I	F	1.47	0.50	3.32	0.73	0.46	0.15	0.15	3.23	0.30	0.08	0.08	7.51
Austral Thrush (<i>Turdus falcklandii</i>)	F(I)	G(F)	0.22	0.78	0.60	—	0.23	0.04	—	0.39	+	0.02	0.02	5.62
Correndera Pipit (<i>Anthus correndera</i>)	I	G	—	—	—	—	—	—	—	—	—	—	—	1.52
Austral Blackbird (<i>Curruca curruca</i>)	I(H)	G	—	+	0.01	—	+	—	—	0.06	—	—	—	1.60
Long-tailed Meadowlark (<i>Sturnella loyca</i>)	I(G)	G	—	—	—	—	—	—	—	+	—	—	—	—
Shiny Cowbird (<i>Molothrus bonariensis</i>)	I(G)	G	—	—	—	—	—	—	—	—	—	—	—	—
Rufous-collared Sparrow (<i>Zonotrichia capensis</i>)	G(H)	G	0.10	1.07	0.03	0.04	0.67	0.48	0.24	0.08	—	0.25	0.25	2.15
Black-chinned Siskin (<i>Carduelis barbatus</i>)	G(H)	G	3.07	1.24	1.30	0.65	2.19	0.14	0.74	1.20	1.84	0.11	0.11	6.50
Yellow-rumped Siskin (<i>Carduelis uropygialis</i>)	G	G	—	—	—	—	—	—	—	—	+	—	—	7.31
Common Djuca-Finch (<i>Djuca diuca</i>)	G	G	0.09	0.07	—	—	0.23	1.66	0.89	—	+	0.62	0.62	5.62
Mourning Sierra-Finch (<i>Phrygilus fruitceti</i>)	G(H)	G	—	—	—	—	0.09	0.35	0.09	0.09	0.81	0.02	0.02	4.05
Plumbeous Sierra-Finch (<i>Phrygilus unicolor</i>)	G	G	—	—	—	—	+	—	—	—	—	—	—	—
Band-tailed Sierra-Finch (<i>Phrygilus ataudinus</i>)	G	G	—	—	—	—	+	+	—	—	—	—	—	—
Gray-hooded Sierra-Finch (<i>Phrygilus gayi</i>)	G(H)	G	0.41	—	—	—	—	—	—	—	—	—	—	—
Patagonian Sierra-Finch (<i>Phrygilus patagonicus</i>)	G(H)	G	—	0.21	0.60	0.23	0.62	—	—	0.05	0.19	—	—	2.27
Density of all birds (ha ⁻¹)			11.74	13.47	20.64	6.93	10.16	5.36	14.35	14.35	6.77	3.36	3.36	3.36
Mean richness (species [2ha] ⁻¹)			12.22	16.41	16.86	8.97	17.63	12.80	15.24	15.24	9.88	8.46	8.46	8.46
Mean diversity (BSD)			2.02	2.26	2.09	1.83	2.41	1.92	2.31	2.31	1.90	1.49	1.49	1.49

* C: Carnivores; F: Frugivores; G: Gramivores; H: Herbivores; I: Insectivores; N: Nectarivores. Secondary diet in parenthesis.
 ** A: Air hunters; F: Foliage gleaners; G: Ground feeders; T: Stem feeders; W: Water feeders. Secondary substrate in parenthesis.
 *** See Methods.
 + Species observed out of the sample. See Results (Birds) for explanation.

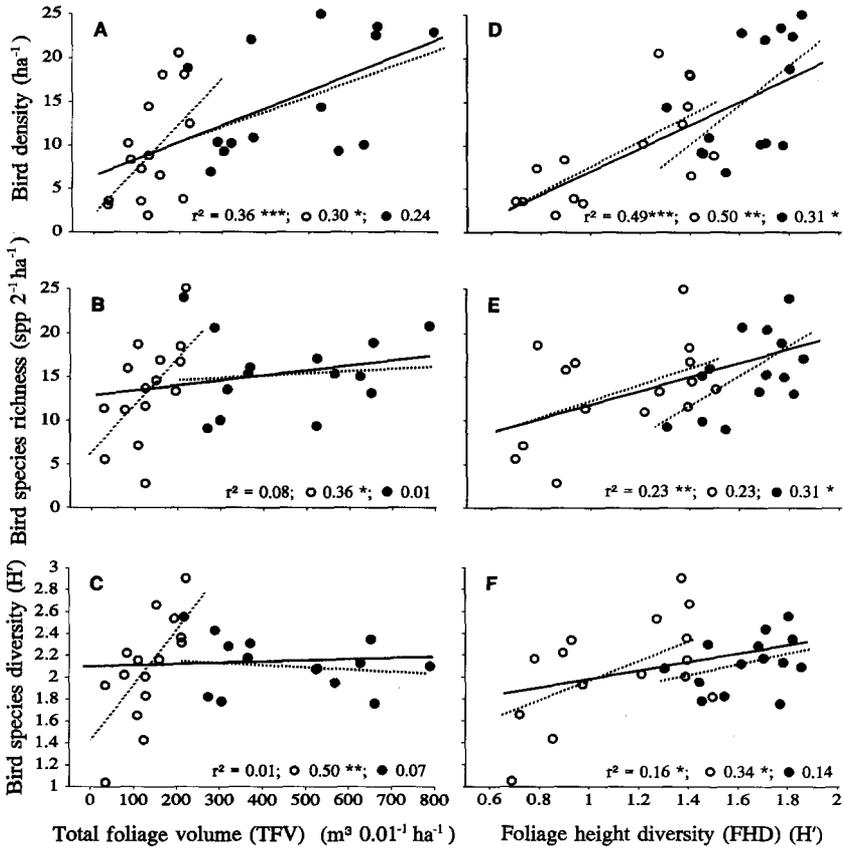


FIGURE 2. Relationships between vegetation variables and bird community variables. The open circles represent the nonforest sites and the black circles, the forest sites. Solid lines represent the least squares regression line for the entire data set; dotted lines represent the least squares regression line for the nonforest and forest sites analyzed separately. The asterisks indicate the statistical significance of correlations (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$).

forests (Table 1). Highest BSD was found in the semideciduous scrub with a mean value of 2.41, whereas the lowest BSD was found at the Poaceae steppe, with only 1.49.

Species with the greatest habitat breadth (B) were the House Wren ($B = 7.51$) and the Black-chinned Siskin ($B = 7.31$), recorded at all habitats, followed by the Rufous-collared Sparrow ($B = 6.50$) and the White-crested Elaenia ($B = 6.47$).

VEGETATION-BIRD COMMUNITY RELATIONSHIPS

Variance in density of all birds per site was highly correlated ($P < 0.001$) with both TFV and FHD (Fig. 2A and 2D, solid lines). Variation of BSR and BSD was only explained significantly by FHD ($P < 0.01$ and $P < 0.05$, respectively;

Fig. 2E and 2F). No significant linear association was found between PSD and any of the bird community parameters. Removing the grassland sites from the model (following Ralph 1985) reduced the amount of variance explained by FHD and TFV for all bird variables. In this case, only the density of all birds was significantly related ($P < 0.01$) with vegetation variables.

Correlations changed substantially when nonforest and forest sites were analyzed separately (Fig. 2, dotted lines). At nonforest sites, all bird community variables were significantly correlated ($P < 0.05$ – 0.01) with TFV (Fig. 2A–2C). FHD significantly explained the variance in density of all birds ($P < 0.01$) and BSD ($P < 0.05$; Fig. 2D and 2F), but failed to explain the variation of BSR (Fig. 2E). At forest sites, no bird community variable was correlated with TFV

(Fig. 2A–2C). FHD was positively correlated with density of all birds ($P < 0.05$; Fig. 2D) and BSR ($P < 0.05$; Fig. 2E) but did not explain BSD's variation (Fig. 2F). Both at nonforest and forest sites, PSD showed no significant correlation with bird community variables.

VEGETATION-BIRD SPECIES RELATIONSHIPS

Over the entire vegetation gradient, several significant correlations were found between vegetation variables and individual bird species. Data concerning these and the following analyses are available from the author on request. TFV and FHD were significantly positively correlated with densities of typical forest bird species (r ranged from 0.43 to 0.68), including the Thorn-tailed Rayadito, the Magellanic Woodpecker, the Patagonian Tyrant, the White-crested Elaenia, the White-throated Treerunner, and the Chucaco Tapaculo. Densities of grassland and scrub species, such as the Common Diuca-Finch and the Long-tailed Meadowlark, were significantly negatively correlated with these vegetation parameters (r ranged from -0.39 to -0.51 , $P < 0.05$ and 0.01 , respectively).

Plant species such as *Chusquea argentina*, *Hypericum perforatum*, *Maytenus disticha*, *Nothofagus obliqua*, and *Ribes punctatum* explained an important part of the variation of forest-bird species densities. On the other hand, plant species such as *Acaena pinnatifida*, *Mulinum spinosum*, and *N. antarctica* were mainly correlated with scrub and openland bird species. The only two significant negative correlations between plant and bird species were found between *Chusquea argentina* and the Rufous-collared Sparrow ($r = -0.40$), and between *N. obliqua* and the Common Diuca-Finch ($r = -0.50$).

Many correlations between birds and vegetation variables changed when nonforest and forest sites were analyzed separately, producing, on average, more bird-plant species relationships and fewer bird-vegetation relationships.

VEGETATION-BIRD GUILDS RELATIONSHIPS

TFV and FHD showed similar overall relationships with the different bird trophic guilds. Densities of primary insectivores, all insectivores, and all frugivores increased significantly as TFV and FHD increased ($P < 0.001$). The latter variables also were highly positively correlated (r

ranged from 0.59 to 0.71; $P < 0.001$) with both primary and all foliage-gleaners.

Foliage volume of the tree *N. obliqua* was positively correlated ($P < 0.001$) with the density of all frugivores, primary and all insectivores, primary and all foliage-gleaners, and all air-hunters (r ranged from 0.58 to 0.70). Significant negative correlations ($P < 0.05$) were found between *Baccharis magellanica* and all granivores, all herbivores, and all foliage-gleaners (r ranged from -0.38 to -0.43).

Correlations of bird guilds and vegetation variables within non-forest sites differed notably from the correlations in forest sites. Few guilds were positively related with FHD in forest sites, but many were at the nonforest sites.

DISCUSSION

Even though FHD and TFV were significantly correlated (Pearson $r = 0.68$; $P < 0.001$) among the 29 sites assessed, they differed in relation to some bird variables (Fig. 2), indicating that these two variables might effectively describe different features of the habitat for certain bird species. For example, species like the Des Mur's Wiretail, the Andean Tapaculo, and the Chestnut-throated Huet-huet, that were influenced by TFV but not by FHD, forage within the densest foliage of the understory. On the other hand, species influenced strongly by FHD, such as the Green-backed Firecrown or the Fire-eyed Diucon, usually hunt for insects flying between trees. Similarly, the Austral Thrush looks for berries in the openings of forests although it also forages in prairies (Table 1). Assemblages of species with such different traits could be responsible for the different patterns observed between the bird communities in forested and non-forested sites.

Results indicate that the relationship of the studied bird communities with the vegetation variables changes with the scale of analysis. Considering the whole vegetation gradient, bird assemblages behaved as predicted by MacArthur and MacArthur (1961), increasing their richness and diversity as FHD increased. However, when grassland sites were deleted from the analysis, no such relationships were found. FHD in non-forest sites was positively related with BSD, but when analyzing the forest plots alone, no significant linear relationship was found between these two variables. These results agree with the patterns observed by Willson (1974).

Whereas along the whole vegetation gradient most bird species tended to be related to structural variables (FHD and/or TFV), within smaller subgroups of sites some bird species were more associated with particular plant species. This pattern has been described before by Rotenberry (1985) in grasslands and by Bersier and Meyer (1994) in forests, and is probably a matter of larger scales masking relationships that exist between birds and individual plant species. Thus, a certain bird species may forage on the insects that live on a certain plant in a shrubland, but in a forest will probably have to select other species that can fulfill its requirements. In both habitats the bird's presence would be associated with one plant species, but such a relationship might not arise along the entire vegetation gradient.

Nonetheless, considering the natural history of the studied bird species, many significant associations found between them and individual plant species lack a known direct cause-effect relationship. However, the relative importance of *N. obliqua* forest for insectivorous birds agrees with the observations of Welch (1988), who concluded that this tree supports higher insect diversity than any other *Nothofagus* in the area.

The patterns described in the Ñuble's bird communities seem to lie between the traditional belief that as foliage diversity increases so does bird community diversity, and the inverse relationship of these two parameters found by Vuilleumier (1972) and Ralph (1985) in Patagonian forests.

Because of their regional isolation, Patagonian forest-bird communities show some characteristics of an island biota, such as a relatively low diversity, and species with wide habitat-niches (Vuilleumier 1985). On the other hand, the steppe and scrubland ecosystems are widespread along the Andes connecting the bird communities with others in South America, thus reducing isolation. However, within the entire range of Patagonian forests, tree species composition varies in important ways. The communities described in Ñuble are at the northern limit of Patagonian forests, and therefore they might show some extreme characteristics. The forests studied by Vuilleumier (1972) and Ralph (1985) were well to the south and lacked *N. obliqua*, a common tree at Ñuble.

Rosenzweig (1995) stated that the birds in the Patagonian *Nothofagus* forests did not seem to

use all the habitat complexity available to them, and Ralph (1985) suggested that this effect was caused by the reduced area and isolation of forests which diminished the number of potential bird species present. But in the present study, the birds did seem to be making some use of the habitat complexity (the estimate of species richness did increase with forest FHD). This local pattern is probably due to the relatively higher insect diversity found in *N. obliqua* forests (Welch 1988) than in other Patagonian and Tasmanian *Nothofagus* forests, where the depauperate insect fauna has been suggested to be a factor in determining the low number of insectivorous birds found in these ecosystems (McQuillan 1993). Thus, even though biogeographic isolation could be ultimately limiting the potential number of bird species present in Patagonian forests, the proximate constraint on most of these forests could be the diversity and abundance of insect prey available to birds, which might be more strongly associated with floristic rather than structural features of the vegetation. Testing this hypothesis remains one of the several tasks that are needed to understand the nature of the forest bird communities of Patagonia.

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