

Does bird species diversity vary among forest types? A local-scale test in Southern Chile

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Abstract Birds are the most diverse vertebrate group in Chile, characterized by low species turnover at the country-size scale (high alpha but low beta diversities), resembling an island biota. We tested whether this low differentiation is valid at a local scale, among six forest habitat types. We detected 25 bird species; avifauna composition was significantly different among habitat types, with five species accounting for 60 % of the dissimilarity. We found a higher level of bird assemblage differentiation across habitats at the local scale than has been found at the country-size scale. Such differentiation might be attributed to structural differences among habitats.

Keywords Beta diversity · Bird community composition · Habitat structure · Island-like biota · Nahuelbuta National Park

Introduction

Biodiversity of Chilean forests resembles an island biota, as they are completely isolated from those of the rest of

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the continent. To the north, the Atacama Desert constitutes a major barrier for species dispersal, to the south lie the Drake Passage and Antarctica, to the east, the Andes range, and to the west, the Pacific Ocean. This isolation explains the current avian biodiversity patterns observed: broad distribution ranges, species-depauperate forests with many endemisms and monotypic genera, which have wide habitat niches and are found along broad latitudinal and altitudinal gradients (Vuilleumier 1985).

Birds are the most diverse vertebrate group in Chile, characterized by a lower species turnover than expected when comparing to areas with similar conditions in North America or Australia, resembling an island biota (Cody 1970). Chilean avifauna, due to its geographical isolation, presents an intermediate endemism level compared to actual island biotas such as Tasmania and New Zealand, concentrating most of the endemisms in a few autochthonous families (Vuilleumier 1985). Further, this group is characterized by a low inter-habitat species turnover along the country (i.e., high alpha [local] diversity, but low beta [regional] diversity), which may be explained by the low habitat specialization observed in Chilean birds (Vuilleumier 1985). Additionally, floristic composition is known to play a major role determining bird diversity throughout Chilean forests, which may explain why many species are common across forest types with contrasting vegetation structure, but sharing key tree species such as *Nothofagus obliqua* (Estades 1997).

The low habitat specialization among Chilean birds may emerge from a character convergence among bird species, where phenotypic divergence has been prevented by natural selection in order to facilitate inter-specific aggregations (i.e., mixed flocks) during the non-breeding season, resulting in a sort of “social mimicry” (Cody 1970). Although Cody (1970) and Vuilleumier (1985) examined this pattern throughout the country, to the best

of our knowledge, its generality has not been tested at a local scale. We sampled birds from six different contiguous forest habitat types in the Nahuelbuta mountain range (southern Chile), aiming to test whether a low species differentiation is also detected at the landscape scale.

Materials and methods

Study area

Our study was conducted in Nahuelbuta National Park (NNP; 37.47° S, 72.60° W; 750–1,550 m a.s.l.), protecting 6,832 ha of the last extant remnants of *Araucaria araucana* and *Nothofagus pumilio* forests on the coastal range of southern Chile. It presents a heterogeneous habitat mosaic with six major forest habitat types classified by their dominant tree species: (1) Roble (*Nothofagus obliqua*)-Ñirre (*N. antarctica*) stands (hereafter RN); (2) Coihue (*N. dombeyi*)-Araucaria (*A. araucana*) stands (CA); (3) mixed Raulí (*N. alpina*) stands (RR); (4) Araucaria-Coihue-Lenga (*N. pumilio*) stands (ACL); (5) Araucaria-Ñirre-Roble stands (ANR); and (6) Raulí-Roble-Avellano (*Gevuina avellana*) stands (RRA) (Fig. S1; Finckh et al. 2000).

Avifaunal assessments

We conducted a quantitative estimation of the presence and relative abundance of non-raptor birds inhabiting the NNP. Bird species richness and abundance were estimated using standardized point counts (Jiménez 2000). At each habitat type, we established ten point-count stations, each separated by 400 m, during the austral spring and summer of 1999 and 2000. At each station, all birds observed visually or aurally within a 40-m radius area and during a 5-min interval were recorded. Bird censuses were conducted during early mornings between 30 min after sunrise and 09:30 am, excluding rainy or windy days. As we did not correct the bird data by detectability, we consider the estimates comparable as relative abundances by species, detected during identical time intervals and sampling areas.

Data analyses

For descriptive purposes, we used species richness and abundance data to calculate the Shannon, species evenness, and Pielou's equitability indices, aiming to compare diversity among habitat types. We assessed the quality of our sampling through the visual inspection of the rarefaction curves based on individuals (Gotelli and Colwell 2001; Colwell et al. 2004). Rarefaction curves were

constructed using Ecosim 7, with 10,000 iterations in each case (Gotelli and Entsminger 2007). An estimate of the expected species richness in each forest type was estimated by the Chao1 abundance-based estimator, calculated in EstimateS 9.1 (Colwell 2013).

To compare the bird community composition among habitat types, we first visually examined the data using a non-metric multidimensional scaling (nMDS) ordination (Legendre and Gallagher 2001; Jiménez et al. 2013). Then, we performed a one-way analysis of similarity (ANOSIM), which is a permutational non-parametric test that operates on similarity matrices (Clarke 1993). Complementarily, we performed a similarity percentage (SIMPER) test aiming to estimate overall dissimilarity among habitat types and also to determine which species were contributing the most to explain compositional differences across habitat types (Jiménez et al. 2013). We used the Bray-Curtis pairwise distance coefficients in all cases. Finally, we estimated species turnover rate (i.e., beta diversity) among habitat types through pairwise comparisons, using Cody's method (Koleff et al. 2003), which is calculated on the mean number of non-shared species between two habitat types (Cody 1975).

Results

We recorded 25 bird species in the study area, with 13–20 species recorded in each habitat type; sampling completeness reached 79–100 %, and expected species richness was 13–24 species across habitats (Table 1). *Elaenia albiceps*,

Table 1 Observed and expected bird species richness for the six habitat types sampled

Habitat type	Number of individuals	Species richness		Sampling effectiveness
		Observed	Expected	
RN	121	19	24	79 %
CA	149	13	13	100 %
ACL	164	19	20	95 %
RR	209	20	23	87 %
ANR	132	14	15	93 %
RRA	148	13	13	100 %

The expected species richness was calculated after the Chao1 estimator. Sampling effectiveness represents the ratio between observed and expected species richness

RN Roble-Ñirre, CA Coihue-Araucaria, ACL Araucaria-Coihue-Lenga, RR mixed Raulí, ANR Araucaria-Ñirre-Roble stand, and RRA Raulí-Roble-Avellano

Sephanoides sephanioides, *Aphrastura spinicauda*, *Scelorchilus rubecula*, *Phrygilus patagonicus*, and *Pygarrhichas albogularis* were present in all habitat types. Conversely, *Veniliornis lignarius*, *Diuca diuca*, *Colaptes pitiús*, and *Cinclodes patagonicus* were found only in one habitat type (Table S1). The highest diversity was found at the RN stand and the lowest at the RRA stand; conversely, CA stand had the highest values of species evenness and equitability and RR stand the lowest ones (Table S2). Rarefaction curves and their 95 % confidence intervals showed a representative sampling for the six habitat types (Fig. 1).

Avifaunal composition among habitat types showed a “core” of shared species, with certain distinctive elements in some habitat types (Fig. 2). Overall, the bird community composition was significantly different among habitats (ANOSIM global $R=0.32$, $p<0.001$), explained by between-habitat pairwise differences detected on each pair of habitat types, except for RR-RRA (Table 2). *Elaenia albiceps*, *Carduelis barbatus*, *S. sephanioides*, *A. spinicauda*, and *S. rubecula* accounted for 60 % of the dissimilarity among habitat types (Table S3). Species turnover among habitat types ranged between 10 and 24 % (Table S4).

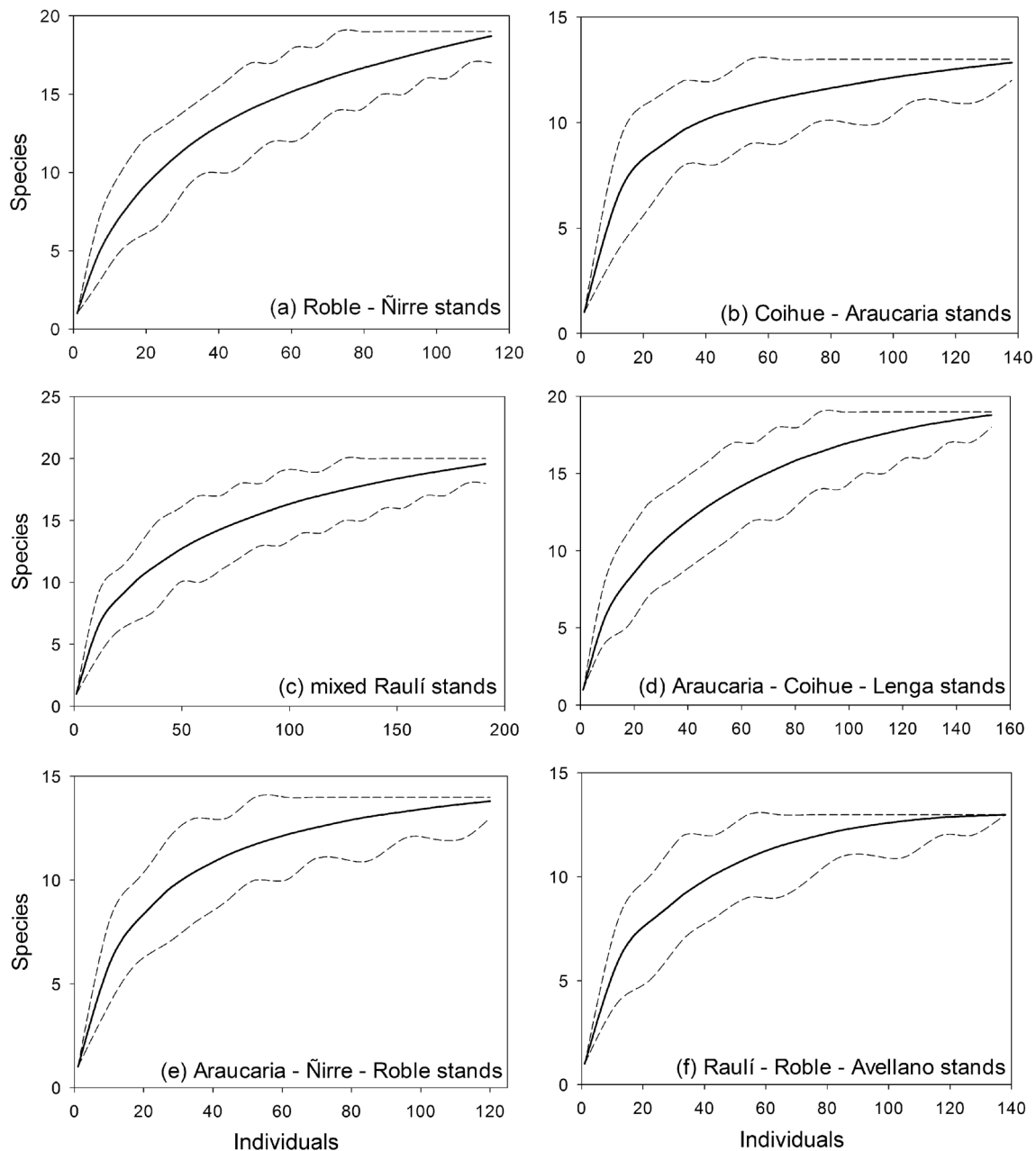


Fig. 1 Rarefaction curves based on individuals (with 95 % confidence intervals) for each sampled habitat type

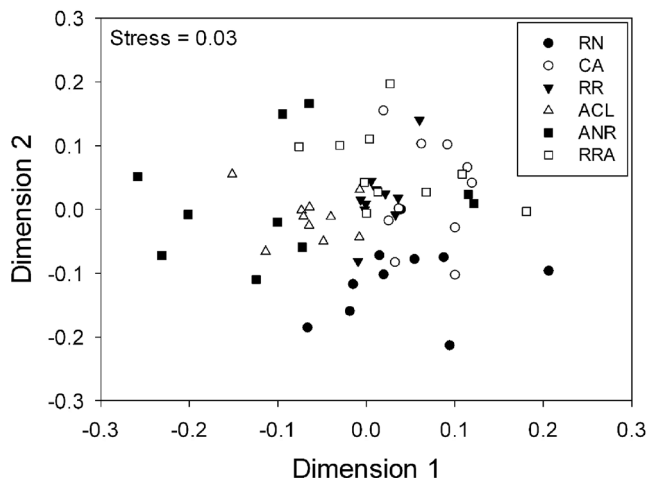


Fig. 2 Non-metric multidimensional scaling plot for species composition (expressed as relative abundances) for the six habitat types assessed (ten censuses per habitat are presented). *RN* Roble-Ñirre, *CA* Coihue-Araucaria, *ACL* Araucaria-Coihue-Lenga, *RR* mixed Raulí, *ANR* Araucaria-Ñirre-Roble stand, and *RRA* Raulí-Roble-Avellano

Discussion

We expected NNP avifauna to be similar among habitat types, considering that these six forest habitat types were adjacent to each other, were non-disturbed, and had no natural or artificial barriers that may have precluded bird dispersal. According to the pattern observed at the countrywide scale, we expected local birds to be “generalist enough” to use all available habitats at the study area. Contrarily to this expectation, we found a species turnover rate of 10–24 % among habitat types; avifaunal composition was significantly different among habitats, except for RR and RRA stands likely because they share Raulí as the main floristic component, being

similar in terms of canopy structure. Nevertheless, species turnover between those two habitat types was 22 %. Estades (1997) argued that the presence of *Nothofagus obliqua* is positively correlated with bird diversity. However, in our results, those stands that include *N. obliqua* as a dominant species (i.e., RN, ANR, and RRA) and those dominated by other *Nothofagus* species (i.e., CA, ACL, and RR) showed similar species diversity and evenness.

On a local scale, structural features are expected to determine the subset of species inhabiting a given habitat due to resource requirements, key structural elements (e.g., perching sites, cavities, fallen logs), and microclimate conditions (Meynard and Quinn 2008). Previous studies on birds in southern Chile demonstrated that avian diversity on a local scale is dependent on forest structure and the successional stage (Reid et al. 2004). Díaz et al. (2005) classified forest bird species either as (1) large-tree users, (2) vertical-profile generalists, (3) understory species, or (4) shrub users. In this sense, the structural differences found in the NNP habitat mosaic may have been related to a differential dominance of some of these groups in different habitats. For example, large-tree users such as *Campephilus magellanicus* and *Pygarrhichas albogularis* were more abundant in stands dominated by *Araucaria araucana* and *Nothofagus dombeyi*, which consist of characteristically tall canopy trees and relatively open understories. Conversely, understory birds such as *Scelorchilus rubecula*, *Pteroptochos tarnii*, and *Sylviorthorhynchus desmursii* were more abundant in stands dominated by *N. alpina* and *N. obliqua*, which have lower canopies, but abundant understory vegetation. Furthermore, vertical-profile generalists such as *Sephanoides sephanioides* and *Turdus falcklandii* showed similar abundances across habitats.

Habitats such as RN, ACL, and RR would allow for greater avian species richness ($S=20\text{--}24$ species) probably due to their greater structural complexity, in comparison to CA, ANR, and RRA ($S=13\text{--}15$ species). Despite that Chilean birds show a low species turnover (i.e., beta diversity) at the country-size scale (Cody 1970), locally, individual bird species do show preferences and avoidances for certain forest habitat types, resulting in a significant differentiation of the avifaunal composition at the local scale. This pattern appears to be associated to the floristic and structural differences among habitat types (Díaz et al. 2005), which stresses the importance of maintaining landscape heterogeneity.

Table 2 Analysis of similarities (ANOSIM) results

Habitat type	RN	CA	RR	ACL	ANR	RRA
RN		0.33	0.29	0.45	0.40	0.42
CA	<0.01		0.26	0.54	0.37	0.25
RR	<0.01	<0.01		0.30	0.37	0.06
ACL	<0.01	<0.01	<0.01		0.27	0.48
ANR	<0.01	<0.01	<0.01	<0.01		0.33
RRA	<0.01	<0.01	0.12	<0.01	<0.01	

Values above the diagonal correspond to the ANOSIM's R -statistic values, and values below the diagonal correspond to p values after a Bonferroni sequential adjustment

RN Roble-Ñirre, *CA* Coihue-Araucaria, *ACL* Araucaria-Coihue-Lenga, *RR* mixed Raulí, *ANR* Araucaria-Ñirre-Roble stand, and *RRA* Raulí-Roble-Avellano

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