

Linking forest structure and composition: avian diversity in successional forests of Chiloé Island, Chile

Iván A. Díaz ^{a,b,*}, Juan J. Armesto ^{a,c}, Sharon Reid ^a,
Kathryn E. Sieving ^b, Mary F. Willson ^d

^a Center for Advanced Studies in Ecology and Biodiversity (CASEB), Pontificia Universidad Católica de Chile, Casilla 114-D, Santiago, Chile

^b Department of Wildlife Ecology and Conservation, University of Florida, 110 Newins-Ziegler Hall, PO Box 110430, Gainesville, FL 32611-0430, USA

^c CMEB, Facultad de Ciencias, Universidad de Chile, Santiago, Chile

^d 5230 Terrace Place, Juneau AK 99801, USA

Abstract

We show how Chilean forest bird species richness, abundance and guild structure changes as a function of structural properties of forest stands. We surveyed bird assemblages in two old-growth (>200 years), two mid-successional (30–60 years), and two early-successional forest stands (4–20 years), from November 1999 to September 2000, on Chiloé Island, southern Chile (42°S). Birds were grouped into four habitat-use guilds: large-tree users, vertical-profile generalists, understory species, and shrub-users that occasionally use forests. We recorded a total of 24 bird species: 21 in old-growth, 14 in mid-successional and 16 in early-successional stands. Large-tree users and understory birds were most abundant in old-growth stands, vertical-profile generalists were common in both old-growth and mid-successional stands, and shrub-users were only common in early-successional stands. For nine bird species we found significant relationships between their local abundance and forest structural elements. Higher bird densities in old-growth forests were associated with greater availability of canopy emergent trees, snags, logs and understory bamboo cover in this habitat. Accordingly, bird species diversity in forest stands can be predicted by the presence of these structural elements, and forests should be managed to conserve structural elements that create favorable habitat for bird species in order to prevent future species losses due to logging practices.

Keywords: Forest structural elements; Forest birds; Chilean temperate rainforests; Understory; Large trees

1. Introduction

In many regions of the world, human exploitation of old-growth forests has greatly altered forest structure over large areas of the landscape (Thiollay, 1992; Berg et al., 1994). The loss of structural components of old-growth forests, such as large canopy trees, logs and snags, is affecting the populations of many species that

depend on these habitat elements (Raphael and White, 1984; Patton, 1992; Newton, 1994; Berg et al., 1994). For example, in Sweden, large, old living trees, logs and snags are critical resources for at least 26% of threatened vertebrate and invertebrate species, particularly birds (Berg et al., 1994). In Guianan rainforest, selective logging decreased the understory cover by 34%, causing a decline in the abundance of understory bird species (Thiollay, 1992). In southeastern Brazil, loss of large canopy trees and understory cover as a consequence of selective logging had negative impacts on the abundances of 21 bird species (Aleixo, 1999).

* Corresponding author. Tel.: +1 352 336 2120; fax: +1 352 846 0527.

E-mail address: diazi@ufl.edu (I.A. Diaz).

In the United States, snags, large trees and the volume of coarse woody debris are important features for many cavity nesters (e.g. Raphael and White, 1984; Walters, 1991; Hutto, 1995; Patton, 1992; Lohr et al., 2002). Therefore, identification of critical structural elements and their relationships to bird species richness and abundance is clearly important for conservation and forest management (Walters, 1991; Patton, 1992; Miller and Marion, 1995; Franklin et al., 1997).

South American temperate rainforests cover a narrow strip along the western margin of southern South America (Armesto et al., 1998). Because of their geographic isolation, these rainforests are characterized by a highly endemic flora and fauna (Armesto et al., 1996a), and are considered as globally threatened ecosystems (Olson and Dinerstein, 1998; Myers et al., 2000). The physiognomy of southern temperate rainforests resembles tropical forests, with a multi-layered canopy composed of evergreen broad-leaved trees, with large emergent canopy trees covered by abundant vines and epiphytes, large biomass of logs and snags, and a dense understory dominated by native bamboos (Veblen et al., 1996; Arroyo et al., 1996; Carmona et al., 2002; Aravena et al., 2002). These forests are inhabited by 44 bird species, with 13 species endemic to south-temperate forests (Vuilleumier, 1985; Rozzi et al., 1996a).

In Chilean temperate rainforests, several studies suggest that forest birds may depend on forest structural elements, particularly understory birds and large-tree users (e.g., Housse, 1945; Goodall et al., 1946; Willson et al., 1994, 1996; McPherson, 1999; Sieving et al., 1996, 2000; Reid et al., 2004; Díaz, accepted). However, in addition to forest clearing, logging practices have created large areas of young forests lacking these structural elements (Donoso and Lara, 1996; Lara et al., 1996; Willson and Armesto, 1996; Aravena et al., 2002). Presently, more than 3.5 million ha (26% of the total forested area of Chile) are covered by various degraded, secondary forests (CONAF-CONAMA-BIRF, 1999), which develop after logging and anthropogenic fire. This modified landscape, dominated by successional forests, may alter regional bird species richness and abundance, changing forest bird assemblages.

In this study, we determined how structural changes in forests, resulting from logging and fire use, affect local species richness and abundance of forest birds. Our goals were: (a) to define 'habitat guilds' (or functional groups) for birds in these rainforests, based on their use of forest microhabitats, (b) to document changes in bird species richness and abundance across a series of successional stands from 4 to 200 years old, and (c) to elucidate the relationships between particular structural components of forests that create bird habitat (e.g., understory, large trees, snags, logs) and bird species abundance. We expected to identify critical relationships between forest

structure and bird habitat that can be used by forest managers in preventing future species losses.

2. Methods

2.1. Study sites

We worked in the landscape surrounding Senda Darwin Biological Station (SDBS), in Chiloé Island, southern Chile (41°50'S, 73°40'W). The area is dominated by fragmented forests of Valdivian and North-Patagonian types (see Veblen et al., 1996) within an anthropogenic matrix of pasture and agricultural fields (Willson and Armesto, 1996). The climate is wet-temperate with a strong oceanic influence (Di Castri and Hajek, 1976), and mean annual precipitation is 2090 mm with a mean annual temperature of 12 °C (SDBS, five year record).

We conducted our study in four large forest fragments (>100 ha each) located nearby SDBS. Inside each fragment, we selected just one, or in some cases, two stands of approx 5 ha. As these stands were part of large forests, they were accessible to the entire pool of forest birds described for the area (see Willson et al., 1994). We selected a total of six stands in the four large forest fragments. We defined their successional stage (years since logging and/or fire) by visual inspections, records from local people and further measures of DBH distribution and tree-ring counts (see below). We chose two stands in each of three successional stages: (i) old-growth (>200 years old), (ii) mid-successional (30–60 years old), and (iii) early successional (4–20 years old). Stands of the same successional stage were separated from one another by at least 2 km. For more detailed description of successional forests in this area see Aravena et al. (2002).

Old-growth forest stands had a canopy dominated by *Drimys winteri* (Winteraceae) *Amomyrtus luma*, *Amomyrtus meli* (both Myrtaceae), *Laureliopsis philippiana* (Monimiaceae), and large emergent *Nothofagus nitida* (Nothofagaceae) and *Eucryphia cordifolia* (Eucryphiaceae). These canopy emergent trees usually have trunk diameters >1 m and the first crown branches are found >20 m above the ground. The canopy of old-growth forests was frequently interrupted by tree-fall gaps (40–200 m²), covered by a dense undergrowth of native bamboo *Chusquea valdiviensis* (Poaceae: Bambusoideae). Mid-successional stands had a more homogeneous and closed canopy, 10–20 m tall, with a greater abundance of shade-intolerant tree species, such as *D. winteri* and *N. nitida*, and a sparse understory cover (Aravena et al., 2002). Early successional stands that had developed after human-induced fires of low intensity were characterized by dense regeneration of shade-intolerant tree species (*D. winteri*, *N. nitida*) 1–3 m tall, and a sparse cover of shrubs, including *Baccharis* spp. (Asteraceae), *Berberis* spp.

(Berberidaceae), and *Gaultheria* spp. (Ericaceae). Pioneer stands often had a few scattered canopy trees and snags that survived anthropogenic fires (Aravena et al., 2002).

2.2. Characterization of stand structure

We used previous studies of bird distributions in Chiloé forests (Willson et al., 1994, 1996; Sieving et al., 2000) to identify potential structural elements or properties of forests that could be important for bird habitat. The apparent dominant factors influencing forest bird habitat are availability of large trees (larger than 60 cm DBH) (e.g. Willson et al., 1994; McBride, 2000), dense understory (Sieving et al., 1996, 2000; Reid et al., 2004), fallen logs (McPherson, 1999), logs and snags (Willson et al., 1994; McPherson, 1999; DeSanto et al., 2002) and tree density (Estades, 1994; Sieving et al., 1996; Díaz and Armesto, 2003). We quantified the abundance of these elements to empirically assess their importance for birds. For each stand we estimated (i) the density of all trees more than 10 cm DBH (diameter at breast height, defined as 1.4 m), (ii) the volume of understory vegetation (bamboo and tree saplings up to 2 m height), (iii) the number of large (more than 20 cm trunk diameter) fallen logs, and (iv) the abundance of snags. The density of trees was estimated using the point-quarter method described in Mueller-Dombois and Ellenberg (1974). We established six sampling points per stand (e.g., 24 trees sampled per stand) along a 100-m transect, with each point 20 m from the next. Data from 24 trees >10 cm DBH in each stand were used to estimate basal area, DBH distributions, and tree species composition. In addition, for each point along the transect we visually estimated the percent canopy cover above 10 m, in an area of 10 m radius assigning each point to one of five canopy cover classes: 0%, 0–25%, 25–50%, 50–75% and >75% cover.

To calculate the volume of understory vegetation of each stand, we established a circle of 2-m radius at each of the six points along the 100 m transect. In each circle we calculated the understory volume using the following equation:

$$U = (h * (\pi r^2)) * c,$$

where U is the volume of understory (m^3) in the 2-m radius circle, h is the height of the understory vegetation (m), r is the radius of the sampling circle (i.e. 2 m), and c is the visually estimated proportion (from 0 to 1) of the circular area covered by the understory growth (see Reid et al., 2004 for similar method). The total volume of understory vegetation per stand was the average of the six sampling points.

The density of fallen logs, with a diameter >20 cm, was equal to the number of logs that crossed the 100-m transect line in each of the six stands. This diameter for logs was chosen because logs with smaller diameters

are seldom used as a nesting site or refuge by birds. Finally, we measured the DBH of all snags located within a 20-m wide strip along the 100 m transect of each stand. To compare among stands, we estimated snag abundance as the number of snags per hectare.

2.3. Habitat-use guilds

Habitat-use guilds were defined from our field observations (Díaz et al., unpublished data) and from data collected in previous studies of forest birds in south-central Chile (Housse, 1945; Goodall et al., 1946; Vuilleumier, 1985; Willson et al., 1994, 1996; Rozzi et al., 1996a,b; Sieving et al., 1996, 2000; McPherson, 1999; Cornelius et al., 2000; McBride, 2000; DeSanto et al., 2002; Deferrari et al., 2001; Díaz et al., 2002; Reid et al., 2004). A bird species was included in a given habitat-use guild based on its primary use of forest structure for nesting and/or feeding.

2.4. Bird surveys

In each of the six successional stands, we conducted bird censuses from dawn to around 10 AM, using fixed 25-m-radius point-counts (Ralph et al., 1993). At each point, we recorded all bird species heard and/or seen during an 8-min period. Sampling points were separated by a minimum of 75 m from adjacent points, and were located more than 100 m away from any forest edge with adjacent pastures, to ensure recording species from forest interior (Willson et al., 1994). To assess the minimum number of points needed for detection of 90–100% of all bird species in each stand, we conducted preliminary surveys and constructed cumulative curves of the number of bird species against the number of sample points. The number of points at which this curve reaches a plateau was taken as a sufficient sample size to ensure detection of >90% of bird species. Based on this analysis, we used six sampling points in old-growth forest stands, five points in each mid-successional stand and four points in each early successional stand. Our surveys included all passerines, doves, hummingbirds, and woodpeckers. Raptors were not included because their large home ranges often include non-forest areas.

Bird surveys were conducted from November 1999 to September 2000, including six surveys during the breeding season (November–March) and two surveys during the non-breeding season (April–September). We focused our analysis only on the breeding season, because weather conditions limited the number of suitable census days during the non-breeding season, and most bird species recorded in the breeding season were also present during the non-breeding season. The only exceptions were three migrant species that leave the area during winter (White-crested Elaenia, Patagonian Tyrant and Green-backed Firecrown).

2.5. Statistical analyses

To compare bird species richness among the three types of successional stands, we first assessed whether our sampling effort was sufficient to represent the species richness of each stand sampled. For that, we performed a Monte–Carlo simulation on the total number of species vs. the total number of individuals observed (as a measure of our sampling effort) using the software Eco-sim[®]. Sampling effort is sufficient when the number of species remains constant with increasing number of observed individuals (see Gotelli and Entsminger, 2001 for details). Second, we evaluated whether bird species composition was nested among successional stands, by using a Nested Analysis with a T index, as described by Atmar and Patterson (1993). Lower T indicated a nested distribution of species among sites. Third, we compared the average species richness (number of bird species observed per point per day) among stands performing repeated measures ANOVA. Because data on bird richness were not normally distributed (Kolmogorov–Smirnov test $P > 0.05$), we used a log transformation in all the analyses (Zar, 1996).

Among the three groups of successional forests, we compared the total abundance of birds, the abundance of each habitat-use guild, and the abundance of each single species per stand. For these comparisons, we used repeated measures ANOVA, with LSD post hoc tests. All analyses were conducted using the software Statistica 6.0[®] (StatSoft Inc. Tulsa, OK, USA).

To investigate the relationships between the abundance of each bird species and the availability of critical structural elements of bird habitat in the successional stands, we performed Multiple Regression Analysis, with stepwise procedures. We examined the residuals to determine the normality of the data (Zar, 1996). Spearman's correlation analysis was used for non-normal data and a Pearson's correlation was calculated for normalized data. Independent variables used in the regressions were the volume of total understory, the volume of bamboo understory, the number of logs, number of small snags, number of large snags, the number of small trees and the number of large trees per hectare (see above). We de-

finer “large trees” and “large snags” as individuals with trunks more than 80 cm DBH. This distinction was based on our field observations and published studies on the size of trees most often used by cavity nesters (see Section 2.3). Regressions and correlations were conducted in the software SPSS[®] (SPSS Inc. Chicago, IL, USA).

3. Results

3.1. Stand structures

Forest stands differed markedly in the availability of structural components. Old-growth forest canopy was less dense, with canopy gaps as a result of tree-falls, a broad DBH distribution with frequent snags, large canopy emergents more than 80 cm DBH, and a dense, but patchy, understory cover composed primarily of native bamboo patches and shade-tolerant Myrtaceae saplings (Table 1, Fig. 1). The complex DBH distribution of old-growth forests results from the combination of shade-intolerant emergents and shade-tolerant canopy trees, which form a multi-layered vertical structure (Aravena et al., 2002). Mid-successional forests presented a narrower DBH distribution, with all trees concentrated in diameter classes less than 40 cm, and a high density of young trees, which generated a closed canopy without canopy gaps (Fig. 1). Understory volume was lower in second-growth stands, characterized by sparse ferns (*Blechnum* spp., Blechnaceae), shade-tolerant tree seedlings and saplings, and few scattered bamboo patches (Table 1). In contrast, early-successional stands presented no continuous canopy cover, few and scattered large trees that were survivors from the fires that started secondary succession, and a fairly large number of snags of different size classes (Table 1, Fig. 1). The understory of early successional sites was composed of a few bamboo patches and up to 50% by ferns and low shrubs (1 m tall), such as *Baccharis patagonica*, *Berberis darwini*, *Berberis buxifolia* and *Gaultheria mucronata*. There were a number of juvenile trees of *Drimys winteri* and *Nothofagus nitida*, often established on piles of woody detritus (Papic, 2000).

Table 1

Availability of forest structural components (means \pm 1 SD) that provide habitat for bird species (see text) in successional forests stands in Chiloé Island

	Old-growth	Mid-successional	Early-successional
Number of trees > 10 DBH (individuals/ha)	576 \pm 361	1680 \pm 1064	4 \pm 5
Basal area of trees > 10 cm DBH (m ² /ha)	95.5 \pm 38.9	48.0 \pm 38.2	2.3 \pm 3.2
Number of trees > 80 DBH (individuals/ha)	42 \pm 10	0	0
Basal area of trees > 80 cm DBH (m ² /ha)	16.2 \pm 0.54	0	0
Understory volume (m ³ /plot \pm 1 SD)	23.2 \pm 1.5	5.9 \pm 4.9	3.5 \pm 1.4
Bamboo volume (m ³ /plot \pm 1 SD)	20 \pm 6.1	0.13 \pm 0.1	<0.1
Logs (number of logs per transect)	7.5 \pm 0.7	2.0 \pm 1.4	4 \pm 2.8
Snags > 10 cm DBH	300 \pm 71	75 \pm 35	800 \pm 566
Percent canopy cover (>10 m height)	50–75	>75	0

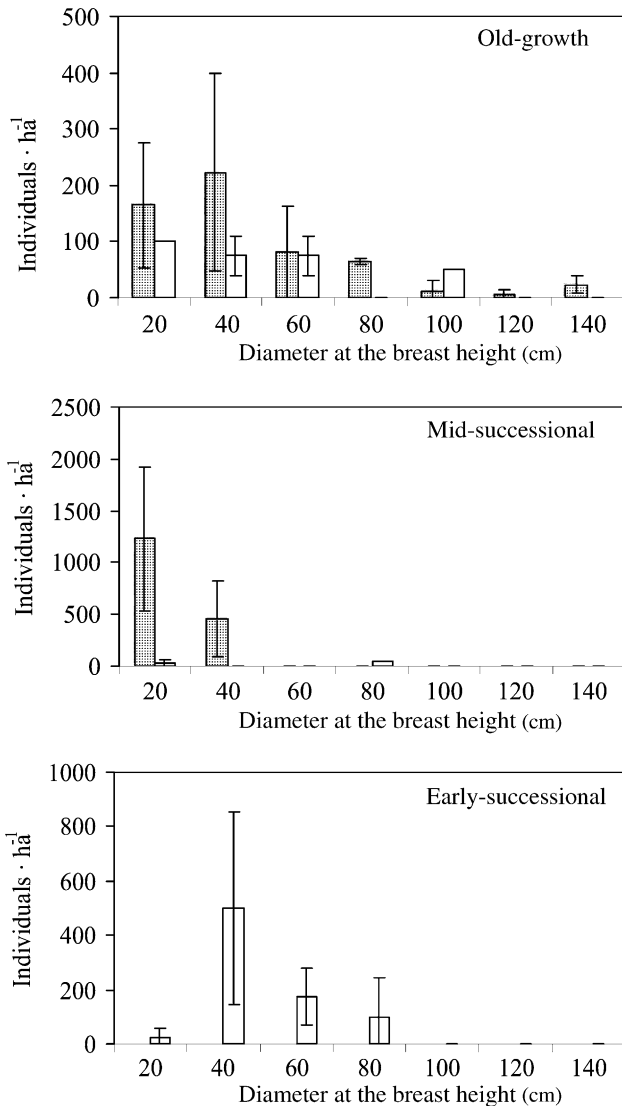


Fig. 1. DBH (diameter at breast height) distribution (means \pm 1 SD) of trees (shaded bars) and snags (open bars) in old-growth, mid-successional and early successional forest stands in Chiloé Island, southern Chile.

3.2. Bird diversity

We identified 24 bird species in our surveys (Appendix A). Ten species were endemic to south-temperate rainforests and another ten species also inhabit a variety of habitats restricted to southern South America (Appendix A). Species accumulation curves indicated that our surveys were sufficient to provide a complete characterization of bird species assemblages in each stand (Fig. 2). Overall, the highest number of bird species was found in old-growth forests, with 21 species recorded in each stand. Mid-successional forests had the lowest number of bird species (11 and 14 species per stand, 14 overall), while early-successional forests had intermediate numbers of bird species (15 and 16 species respectively, 16 species overall; Fig. 2). Birds present in

mid and early successional forests were a subset of the bird assemblage that characterized old-growth forests in the area (Nested analysis $T = 17.5^\circ$, $P = 0.003$).

The average species richness (bird species number per point per day) in old-growth forests was twice the recorded number of species in mid and early successional stands (Fig. 3). Similarly, bird abundance (number of individuals per point per day) decreased from 8.5 in old-growth forest to around 3.0–3.6 in mid and early-successional stands (Fig. 3).

3.3. Habitat-use guilds in successional forests

Based on information of habitat use described by previous authors, we identified four principal habitat-use guilds (Table 2): The first category, “Understory-birds”, was composed of species frequently observed seeking refuge, nesting and feeding under the dense understory vegetation, especially bamboos. Four Tapaculos and the Des Murs’ Wiretail comprised this guild; all of them fly poorly and are restricted to the ground and low vegetation (Willson et al., 1994; Sieving et al., 1996, 2000; Reid et al., 2004; Díaz, accepted). The second guild, “Large-tree users”, was composed of species primarily feeding and nesting in tall trees or snags. Six species comprised this guild; examples are the Magellanic Woodpecker, the White-throated Treerunner and the Slender-billed Parakeet, which are reported as nesting exclusively in large trees (Goodall et al., 1946; McBride, 2000). The third guild, the “Vertical-profile generalists”, were species that use the entire vertical profile of the forest (including canopy and subcanopy vegetation). Nine species comprised this guild (Table 2). Finally, the “Shrub-users” guild was composed of species that are found primarily in open shrublands, but occasionally occur in forests. Four species composed this guild, including the southern House Wren and the Black-chinned Siskin; both are also common in urban areas (Díaz and Armesto, 2003).

3.4. Relationships between bird species abundance and forest structure

Large-tree users were largely restricted to old-growth forests (Fig. 4), with two species absent from younger stands (Appendix A) and the other four species occasionally present in early-successional stands. For instance, the Slender-billed Parakeet and Chilean Flicker were occasionally feeding on scattered snags and tall living trees that survived the disturbance. Vertical-profile generalists were more common in old-growth and mid-successional stands, associated with the development of profuse branching and canopy foliage, but were infrequent in early successional stands with sparse tree cover (Fig. 4). In old-growth and mid-successional forests two vertical-profile generalists,

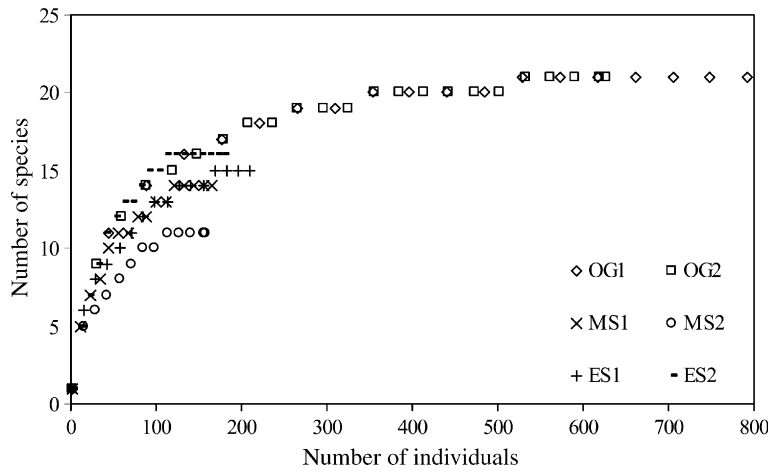


Fig. 2. Cumulative number of species vs. cumulative number of individuals for all census dates in successional forest stands in northern Chiloé Island. Curves were generated by Monte-Carlo simulations (see Gotelli and Entsminger, 2001). Abbreviations: OG1, old-growth forest stand 1; OG2, old-growth forest stand 2; MS1, Mid-successional forest stand 1; MS2, Mid-successional forest stand 2; ES1, early-successional forest stand 1; ES2, early-successional forest stand 2.

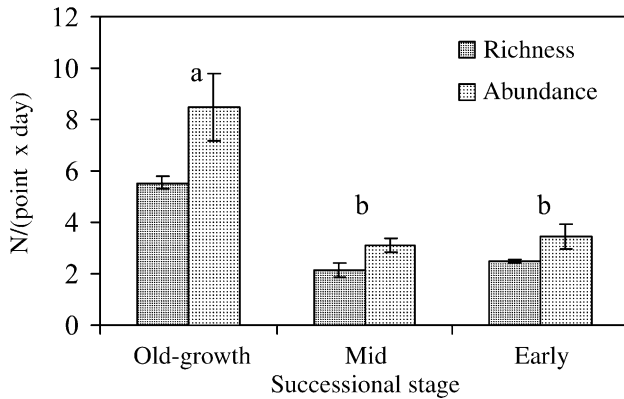


Fig. 3. Mean bird species richness and mean bird species abundance in successional forest stands in Chiloé Island, southern Chile. Different letters above each bar indicate significant differences at $\alpha = 0.05$ (repeated measures ANOVA, $F_{2,5} > 27.1$, $P < 0.01$, LSD post hoc test, $P < 0.05$).

the White-crested Elaenia and the Green-backed Firecrown, were the most abundant bird species (Appendix A).

Understory birds were notably more rich and abundant in old-growth stands (Fig. 4, Appendix A). Two understory species, Des Murs' Wiretail and Magellanic Tapaculo, were also found in early successional stands, where we observed them on log piles, scattered bamboo thickets, and shrub patches. On the other hand, the shrub-users Southern House Wren and Plain-mantled Tit-spinetail, which are common in bushes and in agricultural fields (Goodall et al., 1946; Cornelius et al., 2000; Díaz and Armesto, 2003), were present almost exclusively in early successional sites (Appendix A), often on shrub patches and piles of woody debris. Only one shrub-user species (the Tufted-tit Tyrant) also used old-growth forests (Appendix A).

Table 2
Bird species belonging to the four habitat-use guilds defined in this study

Habitat-use guilds			
Understory species	Large-tree users	Vertical-profile generalists	Shrub-users
• Ochre-flanked Tapaculo (<i>Eugralla paradoxa</i>)	• Magellanic Woodpecker (<i>Campephilus magellanicus</i>)	• Austral Blackbird (<i>Curaeus curaeus</i>)	• Tufted Tit-Tyrant (<i>Anairetes parulus</i>)
• Black-throated Huet-huet (<i>Pterotochos tarnii</i>)	• Chilean Flicker (<i>Colaptes pitius</i>)	• Patagonian Tyrant (<i>Colorhamphus parvirostris</i>)	• Southern House Wren (<i>Troglodytes aedon</i>)
• Magellanic Tapaculo (<i>Scytalopus magellanicus</i>)	• Slender-billed Parakeet (<i>Enicognathus leptorhynchus</i>)	• Chilean Pigeon (<i>Columba araucana</i>)	• Plain-mantled Tit-spinetail (<i>Leptasthenura aegithaloides</i>)
• Chucao Tapaculo (<i>Scelorchilus rubecula</i>)	• White-throated Treerunner (<i>Pygarrhichas albogularis</i>)	• White-Crested Elaenia (<i>Elaenia albiceps</i>)	• Black-chinned Siskin (<i>Carduelis barbata</i>)
• Des Murs' Wiretail (<i>Sylviorhynchus desmursii</i>)	• Chilean Swallow (<i>Tachycineta meyeni</i>)	• Patagonian Sierra-Finch (<i>Phrygilus patagonicus</i>)	
	• Thorn-tailed Rayadito (<i>Aphrastura spinicauda</i>)	• Striped Woodpecker (<i>Picooides lignarius</i>)	
		• Green-backed Firecrown (<i>Sephanoides sephanioides</i>)	
		• Austral Thrush (<i>Turdus falcklandii</i>)	
		• Fire-eyed Diucon (<i>Xolmis pyrope</i>)	

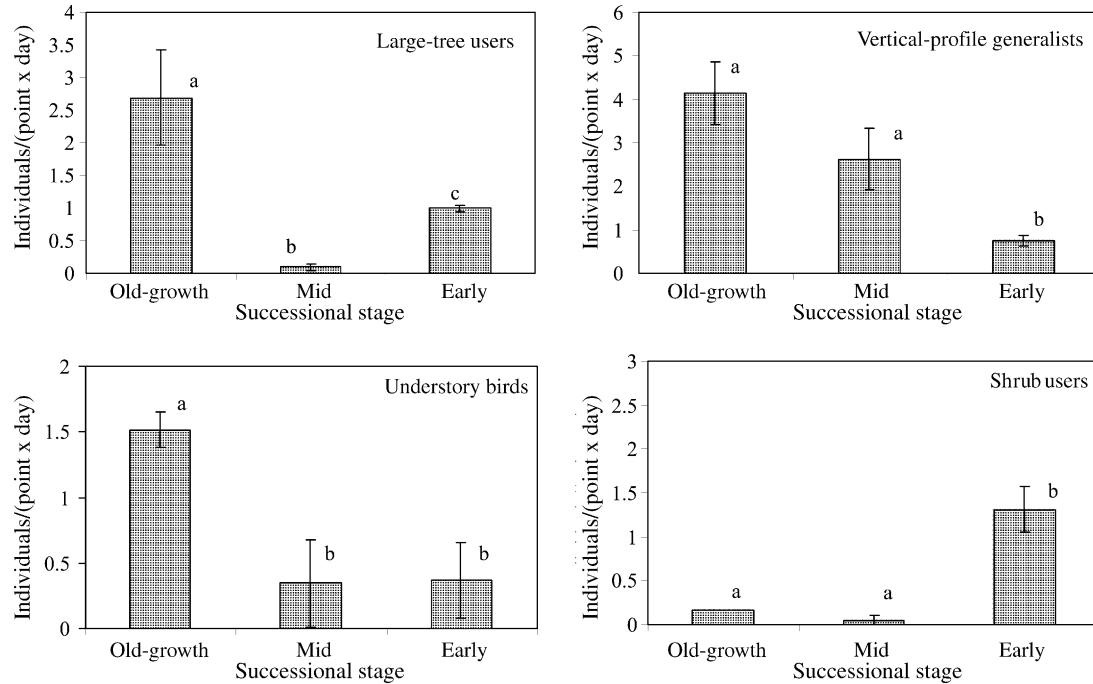


Fig. 4. Abundance of birds (number of birds/point/day) for each habitat-use guild in successional forests in northern Chiloé Island. Letters above the bars indicate significant differences among forests (ANOVA $F_{2,5} > 20.4$, $P < 0.01$, LSD post hoc tests, $P < 0.005$).

The regression analyses between bird abundances and availability of forest structures that create bird habitat (large trees, snags, logs and understory) showed statistically significant relationships for nine species. Abundance of four large-tree users increased linearly as a function of the number of trees more than 80 cm DBH (Pearson $R^2 > 0.9$, $n = 6$ sites, $P < 0.05$). Abundance of most species in the guild of vertical-profile generalists showed no correlation with structural forest elements that we quantified. The exceptions were the Chilean Pigeon and the Green-backed Firecrown, whose abundances were positively correlated with the abundance of trees more than 80 cm DBH (Spearman $R = 0.826$, $P < 0.041$; Pearson $R = 0.961$, $P < 0.002$). The abundances of two understory birds (Chucao Tapaculo and Ochre-flanked Tapaculo) increased significantly with the volume of bamboo understory, while the abundance of the third one (Magellanic Tapaculo) increased significantly with the number of logs per transect ($R > 0.81$, $P < 0.05$). Finally, only one shrub-user (Southern House Wren) showed a negative relationship with forest understory volume ($R = -0.98$, $P = 0.032$).

4. Discussion

4.1. Relationships between bird abundance and forest structure

Despite the small number of trees sampled per stand (see Mueller-Dombois and Ellenberg, 1974 for method-

ological limitations), our results suggest strong influences of local forest structure on bird species richness and abundance, particularly for large-tree users and terrestrial understory birds. These two guilds of birds were most abundant in old-growth forest stands, presumably in response to the greater abundance of large emergent canopy trees, the greater number of standing and fallen dead trees, and the denser bamboo cover that develops under tree-fall gaps. Large trees can benefit birds by offering nesting sites for cavity nesters (Newton, 1994; Berg et al., 1994), and also may support abundant resources for birds such as arthropods in bark, dead woody tissues and in the dense epiphytic layer that covers most of the tall branches (Nadkarni and Matelson, 1989; Nadkarni and Longino, 1990; Sillett, 1994). In secondary forests, these important resources are absent, as is the animal community dependent on them (Nadkarni et al., 2004). This could explain the low abundance of birds that we recorded in secondary forests.

Large-tree users and understory birds were also recorded in early successional forests, despite their absence from young, mid-successional forest stands. Their presence in recently disturbed sites may be associated with structural elements that persisted after disturbance; i.e., “biological legacies” (Perry and Amaranthus, 1997). These legacies include large surviving trees, large snags, logs and bamboo thickets (Carmona et al., 2002; Aravena et al., 2002). However, as early-successional stands grow to their mid-successional phase in 30–60 years, these biological legacies

are gradually lost due to their susceptibility to strong winds, removal by local landowners and decay (Carmona et al., 2002). Thus, mid-successional forests have the lowest avian species richness, almost entirely lacking representatives of two of the four habitat guilds, large-tree users and understory birds. As expected, the density of large trees in the stands was a good predictor of the abundance of large-tree users.

Dense bamboo understory and the presence of logs were good predictors of the abundance of understory species. Understory birds were more abundant in old-growth than in mid-successional stands, where understory vegetation was nearly absent. They were also rare in early successional stands, despite their well-developed shrub cover below 1 m. A recent study suggests that bamboo patches provide more food resources and better protection from predators than other types of low-level vegetation (Reid et al., 2004), and bamboo was the dominant understory vegetation in old-growth stands but not in mid or early successional stands. One understory species (Black-throated Huet-huet) may not depend on bamboo cover for foraging, since it has been frequently observed feeding and perching under a variety of understory vegetation (Reid et al., 2004); however, our field observations indicate they use understory cover to escape from predators. Further studies are needed to elucidate habitat relationships of the Black-throated Huet-huet.

In contrast to large-tree users and understory birds, forest structural elements were poor predictors of the abundance of vertical-profile generalists. These species were present in all successional stands, and were dominant in mid-successional stands, where two species (White-crested Elaenia and Green-backed Firecrown) accounted for 60% of all censused birds (Appendix A). However, Green-backed Firecrown showed a significant association with large trees, which may be due to the large number of epiphytes with nectar-producing, red tubular flowers that cover large trees (Armesto et al., 1996b; Muñoz et al., 2004). Some vertical-profile generalists also use shrublands, agricultural fields, and city gardens to a limited extent (Estades, 1994; Cornelius et al., 2000; Egli and Aguirre, 2000; Díaz et al., 2002; Díaz and Armesto, 2003).

4.2. Implications for conservation

Chilean native forests have been eradicated and degraded at increasing rates over the 20th century, and are now considered a globally endangered ecosystem (Armesto et al., 1998; Myers et al., 2000). Forest management has changed from small-scale traditional selective logging to large-scale logging of all valuable timber species, clearing of forests by use of fire, and

replacement of native forests by forestry monocultures and crop plantations (e.g. Bustamante and Castor, 1998). Traditional selective logging creates small disturbances that resemble the natural disturbance regime (Willson and Armesto, 1996), characterized by a high frequency of small and medium size (<1000 m²) tree-fall gaps (Veblen, 1985; Armesto and Fuentes, 1988). This practice may allow the persistence of critical structural elements that define microhabitats for bird species inhabiting old-growth forests, such as large canopy trees, snags, and bamboo patches in the understory. In contrast, current practices tend to simplify forest structure over large areas, by reducing complex multi-layered forests to stands of simple, even-aged structure (e.g. Oliver and Larson, 1980; Schmidt and Urzúa, 1982; GTZ-CONAF, 1999). Loss of forest structure is responsible for losses of biodiversity in managed forests throughout the world (Thiollay, 1992; Berg et al., 1994; Kohm and Franklin, 1997).

Simplification of forest habitat is an accepted method under most forestry practices and is promoted by the Chilean Forest Service to be applied in most remaining forests in southern Chile (Chilean Forestry Law, currently under discussion in the Chilean Congress). Based on our results, we argue that these practices, if generalized, will likely lead to a sharp decline in regional bird species richness and abundance, particularly for some habitat-use guilds, such as large-tree users and understory birds, but can also affect vertical-profile users. As logging expands, the representation of mid-successional, young stands in the landscape will probably increase, while the area of old-growth forest will shrink (Kohm and Franklin, 1997). We have shown that mid-successional forests have a poor representation of the guilds of large-tree users and understory birds, despite their vicinity to old-growth forests. Consequently, we can proximately a decline in these two habitat-use guilds. Forest growth models indicate that mid-successional stands represent the most persistent stage in a totally managed landscape (Kohm and Franklin, 1997), which worsens the expectations for regional persistence of these two guilds.

The use of forest structural elements has practical advantages for managing bird habitat over indexes of foliage height diversity (Poulsen, 2002). Foliage height diversity indexes have been widely used (MacArthur and MacArthur, 1961; Holmes et al., 1979) but are not always a good predictor of bird diversity as they hide factors such as tree composition, height, or bark and trunk features, which also contribute to bird diversity (Brokaw and Lent, 1999; Poulsen, 2002). In south-temperate rainforests, large canopy trees, snags, logs and bamboo understory are elements that can be easily recognized and quantified by

researchers and managers, facilitating the design of management plans that enhance bird conservation.

The maintenance of forest structural elements will likely permit the conservation of forest birds in managed forests. Silvicultural practices that maintain these elements should be enforced in Chilean forests that are harvested for timber (for examples see, Donoso and Lara, 1999; Atlegrim and Sjöberg, 2004). Logging practices that simulate the local disturbance regime and allow for the maintenance of physical components of bird habitat should be adopted (e.g. Franklin and Armesto, 1996), thus enhancing the conservation of this highly endemic and regionally endangered avifauna (Stattersfield et al., 1998).

Acknowledgements

We thank C.G. Jones for valuable comments and discussions. We are also grateful to M. Machicote, M. Milleson, G.A. Jones, T. Darnell, J. Kappes, M. Reetz, N. Brokaw and especially to T. Contreras for their help in preparing the final version of the manuscript. We also thank all landowners that allowed us to work in their forests. This work is a contribution to the research program of Senda Darwin Biological Station, and was funded by an endowed Presidential Chair in Science to JJA, by Millenium Nucleus P99-103 FICM, and by grant FONDAP-FONDECYT 1501-0001 to the Center for Advanced Studies in Ecology and Biodiversity.

Appendix A

Mean abundance (individuals/point/day \pm 1 SD) of bird species in successional forests, Chiloé Island, southern Chile. Different superscripts indicate significant differences among successional stages ($P < 0.05$; LSD multiple comparison post hoc test). Geographic distribution classes: E, Endemic to southern temperate rainforest; SSA, southern South American; SA, South American; PA, Pan American. Distribution classes follow Rozzi et al. (1996a).

	Geographic distribution	Successional stage		
		Old-growth	Mid-successional	Early successional
Columbidae				
<i>Columba araucana</i>	SSA	0.06 \pm 0.02	0	0.02 \pm 0.03
Emberizidae				
<i>Curaeus curaeus</i>	SSA	0.23 \pm 0.14	0.15 \pm 0.1	0.12 \pm 0.17
Fringillidae				
<i>Phrygilus patagonicus</i>	E	0.1 \pm 0.06	0.04 \pm 0.06	0.16 \pm 0.01
<i>Carduelis barbata</i>	SSA	0	0	0.08 \pm 0.12
Furnariidae				
<i>Aphrastura spinicauda</i>	E	1.14 \pm 0.45 ^a	0.04 \pm 0.06 ^b	0 ^b
<i>Pygarrhynchus albogularis</i>	E	0.05 \pm 0.07	0	0
<i>Leptasthenura aegithaloides</i>	SSA	0 ^a	0 ^a	0.03 \pm 0.05 ^b
<i>Sylviorthorhynchus desmursii</i>	E	0.34 \pm 0.21	0.02 \pm 0.03	0.31 \pm 0.26
Hirundinidae				
<i>Tachycineta meyeri</i>	SA	0.98 \pm 0.05 ^a	0.05 \pm 0.01 ^b	0.81 \pm 0.14 ^a
Muscicapidae				
<i>Turdus falcklandii</i>	SSA	0.35 \pm 0.31	0.2 \pm 0.12	0.06 \pm 0.03
Rhinocryptidae				
<i>Eugralla paradoxa</i>	E	0.07 \pm 0.1	0	0
<i>Pterotochos tarnii</i>	E	0.16 \pm 0.12	0.08 \pm 0.12	0
<i>Scelorchilus rubecula</i>	E	0.81 \pm 0.06 ^a	0.22 \pm 0.16 ^b	0 ^b
<i>Scytalopus magellanicus</i>	SSA	0.14 \pm 0.12	0.02 \pm 0.03	0.06 \pm 0.03
Troglodytidae				
<i>Troglodytes aedon</i>	PA	0 ^a	0 ^a	1.06 \pm 0.33 ^b
Tyrannidae				
<i>Anairetes parulus</i>	SA	0.16 \pm 0.01	0.04 \pm 0.06	0.21 \pm 0.11
<i>Colorhamphus parvirostris</i>	E	0.02 \pm 0.03	0	0
<i>Elaenia albiceps</i>	SA	1.9 \pm 0.4 ^a	1.74 \pm 0.68 ^a	0.21 \pm 0.34 ^b
<i>Xolmis pyrope</i>	SSA	0.01 \pm 0.02	0.04 \pm 0.06	0
Picidae				
<i>Campephilus magellanicus</i>	E	0.04 \pm 0.05	0	0
<i>Colaptes pitius</i>	SSA	0.06 \pm 0.05	0	0.08 \pm 0.12
<i>Picoides lignarius</i>	SSA	0.03 \pm 0.04	0.02 \pm 0.03	0.02 \pm 0.03

Appendix A (continued)

	Geographic distribution	Successional stage		
		Old-growth	Mid-successional	Early successional
Psittacidae				
<i>Enicognathus leptorhynchus</i>	E	0.42 ± 0.17 ^a	0 ^b	0.1 ± 0.03 ^b
Trochilidae				
<i>Sephanoides sephaniodes</i>	SSA	1.5 ± 0.09 ^a	0.42 ± 0.19 ^b	0.08 ± 0 ^b
Total		8.5 ± 1.3 ^a	3.09 ± 0.26 ^b	3.4 ± 0.48 ^b

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