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IMPORTANCE OF NATIVE BAMBOO FOR UNDERSTORY BIRDS IN CHILEAN TEMPERATE FORESTS

Sharon Reid,[1,2,5] Iván A. Díaz,[1,3] Juan J. Armesto,[1,2] and Mary F. Willson[4]

[1]*Center for Advanced Studies in Ecology and Biodiversity (CASEB), Pontificia Universidad Católica de Chile, Casilla 114-D, Santiago, Chile;*
[2]*Laboratorio de Sistemática y Ecología Vegetal, Facultad de Ciencias, Departamento de Biología, Universidad de Chile, Casilla 653, Santiago, Chile;*
[3]*Department of Wildlife Ecology and Conservation, University of Florida, 110 Newins-Ziegler Hall, P.O. Box 110430, Gainesville, Florida 32611-0430, USA; and*
[4]*5230 Terrace Place, Juneau, Alaska 99801, USA*

Abstract.—In South American temperate rainforests, five endemic understory birds (four Rhinocryptidae and one Furnariidae) are often associated with the main understory plant, the native bamboo *Chusquea valdiviensis* (Poaceae: Bambusoideae). We studied the effects of bamboo cover on species abundance and richness of those understory birds and explored the functions of bamboo as food resource and escape cover. In Chiloé Island (42°S), southern Chile, we selected four old-growth forest patches >100 ha and in each patch conducted bird surveys in six plots with >70% understory cover. Three plots were dominated by native bamboo and three plots had a sparse bamboo cover. Bird abundance (point counts) was significantly correlated with both total understory cover and percentage of bamboo cover but was not correlated with other kinds of understory plant cover. Bird species richness was positively correlated with bamboo cover and negatively correlated with other kinds of understory cover but unrelated to total understory cover. Leaf-gleaners Magellanic Tapaculos (*Scytalopus magellanicus*), Ochre-flanked Tapaculos (*Eugralla paradoxa*), and Des Murs's Wiretails (*Sylviorthorhynchus desmursii*), and the ground-gleaner Chucao Tapaculos (*Scelorchilus rubecula*) were more abundant in high-bamboo plots; but the ground-gleaner Black-throated Huet-huet (*Pteroptochos tarnii*) was recorded more times in plots with low-bamboo cover.

Availability of invertebrates per unit of understory dry mass did not differ between high- and low-bamboo plots; but plant biomass was greater in high-bamboo plots, so total invertebrate abundance per plot was higher there. Ground-litter invertebrate abundance was similar in all plots. To examine escape-cover preferences, nine captured Chucao Tapaculos were released in front of two different understory scenarios (high-bamboo cover or bamboo-free understory); 88% of released birds moved into bamboo cover. We suggest that the structure of native bamboo understory is critical for the maintenance of four of those species, and retaining bamboo cover in managed stands may help minimize the effect of logging on understory birds. *Received 9 May 2003, accepted 19 January 2004.*

Resumen.—En bosques templados de Sudamérica, cinco especies de aves endémicas de sotobosque (cuatro Rhinocryptidae y un Furnariidae) se encuentran frecuentemente asociadas a la principal planta de sotobosque, el bambú nativo *Chusquea valdiviensis* (Poaceae: Bambusoideae). Estudiamos los efectos de la cobertura de *Chusquea* sobre la abundancia y riqueza de especies de estas aves de sotobosque, y exploramos las funciones del bambú como fuente de recursos (alimento) y cobertura de escape. En la isla de Chiloé (42º S), sur de Chile, seleccionamos cuatro parches de bosque primario mayores a 100 ha y en cada parche realizamos censos de aves en seis estaciones con más de 70% de cobertura de sotobosque. Tres estaciones estaban dominadas por *Chusquea* y tres tenían una escasa cobertura de bambú. La abundancia de aves (en estaciones de escucha) estaba positivamente correlacionada con la cobertura total de sotobosque y el porcentaje de cobertura de bambú, pero no presentaba correlación con la cobertura de otras especies de plantas en el sotobosque. La riqueza de especies de aves estaba correlacionada positivamente con la cobertura de bambú y negativamente con la cobertura de otras especies del sotobosque, pero no tuvo relación con la cobertura total del sotobosque. Las especies que se alimentan en el follaje, *Scytalopus magellanicus*, *Eugralla para-*

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[5]E-mail: sreid@bio.puc.cl

doxa y *Sylviorthorhynchus desmursii*, y una especie que forrajea en suelo, *Scelorchilus rubecula*, fueron más abundantes en las estaciones dominadas por bambú, pero otra especie de suelo, *Pteroptochos tarnii*, fue más frecuente en estaciones con escasa cobertura de bambú.

La disponibilidad de invertebrados por unidad de biomasa seca de sotobosque no difirió entre estaciones con dominancia o escasez de bambú, pero la biomasa vegetal fue mayor en las primeras. Por lo tanto, la abundancia total de invertebrados en éstas fue mayor. La abundancia de invertebrados en la hojarasca fue similar en todas las estaciones. Para examinar posibles preferencias de cobertura de escape, se liberaron nueve individuos de *S. rubecula* frente a dos tipos de sotobosque (alta cobertura de bambú o sin bambú); 88% de las aves eligieron cobertura de bambú. Se sugiere que el sotobosque de bambú es crítico para la mantención de cuatro especies de aves, por lo que la retención de cobertura de bambú en bosques manejados puede reducir el impacto de la alteración del hábitat sobre las aves del sotobosque.

Effects of habitat structure on avian populations and mechanisms involved in producing those effects have been considered a primary research area for avian conservation biology (Morrison et al. 1992, Rozzi et al. 1996, Walters 1998). Vegetation structure may provide escape cover against predators, safe nesting sites, and food resources for birds (Feinsinger et al. 1988, Lima 1993). Understanding how understory vegetation structure influences habitat selection by understory birds could help elucidate the mechanistic bases of community organization and structure (Moermond 1990).

South American temperate rainforests cover a narrow area of the Andes between 35°S and 55°S in southern Chile and westernmost Argentina and sustain over 44 bird species; 64% are found only in southern South America and 30% of those are endemic to south-temperate forests (Vuilleumier 1985, Rozzi et al. 1996). Native bamboo (Poaceae: Bambusoideae), typically *Chusquea valdiviensis* (hereafter "bamboo"), dominate the understory, especially under light gaps (Armesto et al. 1996, Matthei 1997). Where forests have been burned or selectively logged, bamboo typically dominates the understory in treefall gaps, forming extensive thickets (Veblen 1982). In industrial exploitations bamboo is often removed from the understory together with other woody residues.

Only in the last decade have studies begun to document the relationship between forest structure and habitat use by avian species in south-temperate forests (Willson et al. 1994, 2001; Sieving et al. 1996, 2000; Díaz 1999; Estades and Temple 1999; Morrison and Phillips 2000; De Santo et al. 2002; I. A. Díaz et al. unpubl. data). Both the landscape configuration of forest patches (fragmentation and isolation) and vertical stratification within patches are predicted to affect avian species abundance and richness (Wiens 1989).

Previous studies in south-temperate forests have suggested that certain forest elements (such as big trees, logs, and understory cover) are important for the presence of a number of species of native birds (Willson et al. 1994, 1996; Sieving et al. 2000; Reid et al. 2002; I. A. Díaz et al. unpubl. data). In particular, bamboo understory apparently is a critical habitat for five endemic species (four Rhinocryptidae and one Furnariidae) of understory birds on Chiloé Island, southern Chile. Bird surveys suggest that the presence and abundance of Chucao and Ochre-flanked tapaculos and Des Murs's Wiretails (scientific names in Table 2) is commonly associated with bamboo cover (Sieving et al. 1996, 2000; Díaz 1999; McPherson 1999; De Santo et al. 2002). Those understory birds are nonmigratory invertebrate-eaters that have poor flying abilities, and their abundance and species richness decreases in small forest fragments in Chiloé Island (Willson et al. 1994). A high proportion of endemic understory birds in the family Rhinocryptidae are considered to be globally endangered (Vuilleumier 1985, Glade 1988, Collar et al. 1992), so understanding the habitat requirements of those birds is important for their conservation.

Considering that rainforests on Chiloé Island and other areas in southern Chile continue to be logged and structurally degraded (Lara et al. 1996, Willson and Armesto 1996), we designed a study to assess and quantify the ecological role of native bamboo in determining the distribution and abundance of the five understory bird species that inhabit temperate lowland rainforests in northern Chiloé Island. Here we ask specifically whether bamboo cover is associated with the presence and abundance of understory birds in southern forests, or whether other types of understory vegetation (e.g. tree saplings) will suffice. In addition, we examined the following hypotheses about the ecological role of bamboos: (1) bamboo habitat provides more food resources to understory birds than bamboo-free understory, and (2) bamboo cover may be selected by birds as a potential escape cover, which could be safer in comparison to other types of understory cover.

Methods

Study area.—The study was conducted in a rural landscape in northeastern Chiloé Island in southern Chile (41°50′S, 73°40′W). The region has been subject to a continuous environmental degradation because of a century of forest logging and land clearing for agricultural use, which has caused intense fragmentation and reduction of forest area (Armesto et al. 1994, 1998; Lara et al. 1996; Willson and Armesto 1996).

Climate is wet-temperate with a strong oceanic influence (Di Castri and Hajek 1976). Annual precipitation is 2,090 mm with a mean annual temperature of 12°C (Senda Darwin Biological Station, five-year record). Forests are dominated by evergreen, broad-leaved trees, and some narrow-leaf conifers (*Saxegothaea conspicua*, *Podocarpus nubigena*). Main emergent trees are *Nothofagus nitida*, *Drimys winteri*, and *Eucryphia cordifolia*. Understory is dominated by bamboo under light gaps, and by shade-tolerant myrtaceous seedlings and saplings, such as *Amomyrtus luma*, *Amomyrtus meli*, and *Myrceugenia parviflora* in shaded areas under the closed canopy.

Study design.—We selected four old-growth forest patches >100 ha using 1:20,000 orthophotos from 1993, named hereafter as "F1", "F2", "F3", and "F4". The size of the forest patches was large enough to avoid possible effects associated with small fragments (see Willson et al. 1994) and also allowed us to find areas with a dense bamboo understory as well as areas with sparse bamboo cover, because of the vast heterogeneity of microhabitats (Freemark and Merriam 1986). In each patch, we established six 50-m-radius sample plots with >70% of the area of the plot covered with understory vegetation (estimated visually by two observers). Bamboo patches within forest fragments varied in size and shape, and it was impossible to establish pure bamboo plots (i.e. no bamboo patch was large enough to cover 100% of a 50-m-radius sample plot). The high frequency of bamboo patches did not allow us to establish bamboo-free plots. Therefore, we established three plots averaging 75% bamboo cover (hereafter "high-bamboo plots"), and three matching plots with dominance of tree seedlings and saplings and a sparse bamboo cover (on average 14% bamboo cover; hereafter "low-bamboo plots"). Canopy tree density and composition was kept as similar as possible between plots, despite the fact that high-bamboo plots were located near or under small tree-fall gaps (Table 1).

Bird surveys.—Bird surveys followed the point-count methodology used in a similar study by Willson et al. (1994), described in Ralph et al. (1993), and were carried out in each of the six 50-m-radius plots in each patch. All understory birds seen or heard within the plots were recorded for an 8-min period. Plots were separated from each other by at least 200 m to minimize the risk of counting the same individual twice (Hutto et al. 1986). Bird surveys were performed from 0730 to 1000 hours EST on no-rain days (Willson et al. 1994). Each plot was surveyed five times during the breeding season, from December 2000 until late March 2001 (i.e. austral spring and summer). We concentrated our sampling effort in the breeding season because of the higher vocalization activity and detectability of those birds. On Chiloé Island, a marked decrease in activity of resident birds in the nonbreeding season increases the chances of underestimating bird species abundance (S. Reid and I. Díaz pers. obs.).

Table 1. Vegetation variables and food resources associated with high- and low-bamboo plots in two forest patches (F1 and F3) in Chiloé Island, southern Chile (mean ± SD).

	Habitat		
Vegetation variables	High-bamboo plots	Low-bamboo plots	*P*
Understory height	2.37 ± 0.27	2.3 ± 0.48	0.783
Total understory cover (%)	83.83 ± 12.3	69.8 ± 21.7	0.207
Bamboo cover (%)	74.5 ± 14.6	14.3 ± 11.9	<0.001
Cover of other understory plants (%)	10.7 ± 5.9	55.8 ± 21.1	<0.001
Canopy cover (%)	37.5 ± 27.4	68.8 ± 15.3	0.034
Number of logs intersecting transects	8.2 ± 3.4	7.7 ± 3.4	0.806
Foliage invertebrates (individuals per plot)	64.4 ± 20.6 × 10^5	17.4 ± 3.4 × 10^5	<0.001

That methodology did not allow us to estimate absolute values of abundance and richness of birds; so for patch comparisons, we considered abundance as the mean number of birds per plot per day and richness as the mean number of species per plot per day. We also analyzed how the maximum abundance and maximum richness of species differs between high- and low-bamboo plots and how they relate to understory and bamboo cover. Maximum abundance was calculated by summing the maximum number of individuals recorded per species in the five surveys and maximum richness was calculated by summing all the species recorded in the five surveys in each plot. We chose that method because we were interested in the maximum number of birds and bird species that potentially use the understory vegetation in the plots, and that allowed comparisons among plot types on the same basis.

Understory characterization.—We characterized the amount and composition of understory cover in two of the four forest patches, F1 and F3 (i.e. 12 plots in total). In each plot, we established two 50-m-long transects perpendicular to each other, centered in the plot and oriented along cardinal points. We then set up five regularly spaced points along those transects (one in the center and the other four in each of the four cardinal points). At each point, two independent observers visually estimated understory height, bamboo cover, other understory cover (i.e. percentage of cover of species other than bamboo) and total understory cover within a 5-m-radius area. All understory and canopy species were recorded and canopy cover above the plots was estimated using four intervals, 0–25%, 25–50%, 50–75%, and 75–100%. The presence of fallen logs >15 cm diameter was recorded when logs intersected the transects; this diameter for logs was chosen because logs with smaller diameters are seldom used as a nesting site by understory birds (S. Reid et al. pers. obs.).

Food availability.—All five understory bird species studied are invertebrate-eaters, although Chucao Tapaculos and Black-throated Huet-huets also consume fruits (Armesto et al. 1987). To test whether bamboo habitat provides more food resources than low-bamboo understory (hypothesis 1), we performed time-constrained searches for invertebrates on understory foliage and ground litter in plots with high- and low-bamboo cover in the same 12 plots where vegetation variables were measured. Invertebrate abundance was used as a substitute for food availability (Griffiths 1975).

For invertebrate abundance on foliage, we randomly chose first eight 1-m-long branches and counted all invertebrates on the branch during a 3-min period. Then, we removed the target branch at its base and later dried it in a Shellab multi-purpose oven model 1350 FX (Sheldon Manufacturing, Cornelius, Oregon), at 50°C for 48 h and weighed it in a Ohaus balance model C305 to estimate number of invertebrates per unit of understory biomass. To estimate invertebrate abundance per plot, we first calculated the biomass of 1 m^3 of bamboo ($n = 5$) and bamboo-free understory ($n = 5$) by removing that volume (defined by a 1 m^3 PVC cube) from the understory with pruning scissors and weighing the oven-dried samples. To estimate total understory biomass in the 50-m-radius plots, we first calculated the total understory volume (bamboo and bamboo-free understory separately) with the following equation $\pi \times r^2 \times h \times (C/100)$, where $\pi = 3.14$, r is the plot radius (i.e. 50 m), h is the average understory height, and C is bamboo and bamboo-free cover, respectively, for each case. Biomass of bamboo and bamboo-free understory per plot was estimated by multiplying the result of that equation with the estimated biomass of 1 m^3 of bamboo and bamboo-free understory, respectively (see above). The sum of biomass of bamboo and bamboo-free species gave us an estimate of the total understory biomass per plot. That result was then multiplied by the mean number of invertebrates in 1 g of biomass of bamboo and bamboo-free species. Abundance of invertebrates associated with understory foliage of high- and low-bamboo plots was analyzed by a one-way ANOVA.

For invertebrates in ground litter, we searched for invertebrates in a rectangle of 7×20 cm (area = 210 cm^2) during an 8-min period and recorded all counted invertebrates (see Willson and Comet 1996 for a similar method). That was repeated randomly eight times per plot in the same two forest patches where understory foliage was sampled. Invertebrate abundance was expressed as number of invertebrates per area of ground litter, and that was extrapolated to the area of the plot. Comparisons between high- and low-bamboo plots were done by a one-way ANOVA.

Bamboo as escape cover.—To test bamboo as a potential escape cover (hypothesis 2), we conducted experiments with nine Chucao Tapaculos captured using a 50 × 40 cm wooden box-trap. We placed a petri dish with bait beneath the box to attract the birds' attention. Common litter invertebrates (such as crickets, larvae, and grubs) were used for bait. Individuals were kept in captivity in the dark inside a 20-cm wide × 20-cm tall × 100-cm long tube, with both ends closed for 5–10 min, for acclimatization. Then, one of the ends was opened, and released birds were faced with two different and equally distanced understory scenarios, one with >80% bamboo cover (visually estimated) and the other with >80% of tree seedlings and saplings. The direction and first perching place after release was recorded. The small number of birds tested reflects the low capture rates.

Data analyses.—We tested for normality of the data using one-sample Kolmogorov-Smirnov tests, with Lilliefors distribution (i.e. standard normal distribution). Survey data were not normally distributed, so comparisons of mean bird abundance among forest patches were done using the nonparametric Kruskal-Wallis test. Our data did not show significant differences between forest patches, so we grouped all high-bamboo plots and all low-bamboo plots separately and compared mean abundance of each species, maximum total abundance, and maximum species richness between those two groups. All comparisons were done by the nonparametric Mann-Whitney *U*-test. To relate maximum species abundance and maximum richness with bamboo cover, we performed regression analyses in the 12 plots where vegetation variables were characterized. To test for bamboo as a major food source, we compared the amount of invertebrates between high- and low-bamboo plots by a one-way ANOVA. To test for bamboo as a preferred cover selection site, we used a sign test on the number of captured birds selecting bamboo. All statistical tests as described in Zar (1984) were performed using SYSTAT 8.0.

Results

Understory characterization.—All four forest patches presented abundant tree-fall gaps and were similar in structure and tree species composition. Understory composition in all patches was characterized by a mosaic of areas dominated by bamboo and areas dominated by myrtaceous tree saplings. Two patches, F1 and F4, presented a more dispersed canopy as a result of old logging practices and fire; in the latter, we did not record two of the five bird species studied, the Black-throated Huet-huet and Ochre-flanked Tapaculo.

High- and low-bamboo plots presented similar total understory cover and number of logs (Table 1). As expected, high-bamboo plots were characterized by a significantly higher bamboo cover ($t = -7.80$, df = 10, $P < 0.001$), whereas low-bamboo plots presented a higher cover of other understory vegetation (i.e. myrtle saplings) and a denser canopy cover ($t = 5.04$, df = 10, $P < 0.001$; $t = 2.45$, df = 10, $P = 0.034$, respectively).

Bird abundance and species richness.—Mean abundance of each species was similar among forest patches (Table 2). Chucao Tapaculos were the most abundant bird species in the understory of all four forest patches, followed by Magellanic Tapaculos and Des Murs's Wiretails. Ochre-flanked Tapaculos were rare in all patches (Table 2). Des Murs's Wiretails and Chucao and Magellanic tapaculos were significantly more abundant in high-bamboo plots ($U = 17$, $P = 0.001$; $U = 25.5$, $P = 0.007$; and $U = 31.5$, $P = 0.016$, respectively). Ochre-flanked Tapaculos were

Table 2. Mean number of individuals per point per day of understory bird species in four forest patches in Chiloé Island (range in parentheses).

Common name	Scientific name	F1	F2	F3	F4	KW[a]	*P*
Des Murs's Wiretail	*Sylviorthorhynchus desmursii*	0.33 (0–2)	0.37 (0–1)	0.27 (0–1)	0.23 (0–2)	0.81	0.847
Black-throated Huet-huet	*Pteroptochos tarnii*	0.17 (0–2)	0.23 (0–2)	0.23 (0–2)	0.0	5.365	0.147
Chucao Tapaculo	*Scelorchilus rubecula*	1.47 (0–3)	1.63 (0–3)	0.97 (0–2)	1.47 (0–4)	4.736	0.192
Ochre-flanked Tapaculo	*Eugralla paradoxa*	0.10 (0–2)	0.03 (0–1)	0.07 (0–1)	0.0	1.11	0.775
Magellanic Tapaculo	*Scytalopus magellanicus*	0.67 (0–2)	0.57 (0–2)	0.47 (0–2)	0.73 (0–2)	3.276	0.351
Total abundance		2.74	2.83	2.01	2.43	0.451	0.93
Total species richness		1.97 (1.2–3.2)	1.97 (1–2.8)	1.67 (0.4–2.8)	1.83 (0.8–2.2)	0.604	0.896

[a] KW = Kruskal-Wallis statistic for differences among forest fragments.

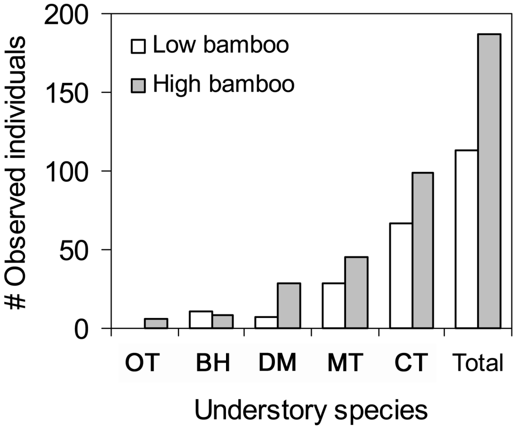

FIG. 1. Total number of birds counted in high and low bamboo plots during the breeding season. Abbreviations: CT = Chucao Tapaculo (n = 166), MT = Magellanic Tapaculo (n = 73), DM = Des Murs's Wiretail (n = 36), BH = Black-throated Huet-huet (n = 19), and OT = Ochre-flanked Tapaculo (n = 6).

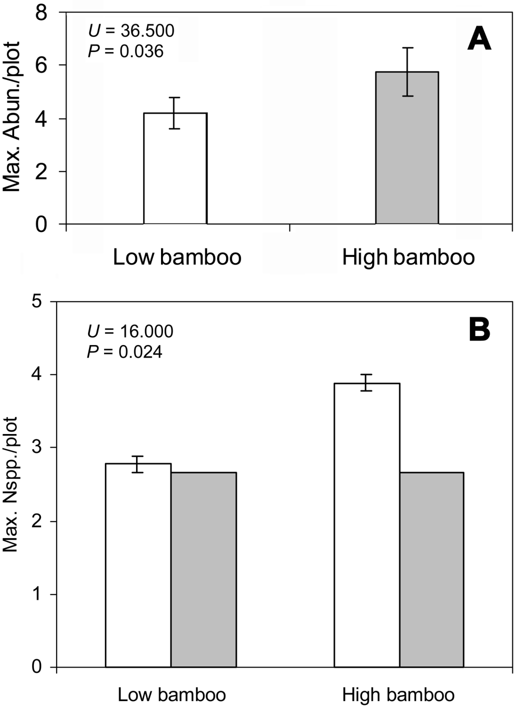

FIG. 2. Relationship between (A) maximum abundance in 12 low- and high-bamboo plots for four forest patches and (B) maximum species richness (N spp.) in 9 low- and high-bamboo plots (three forest patches) and in a degraded forest patch (shaded bar).

never recorded in low-bamboo plots, although recorded individuals were too few to observe a significant difference between plots ($U = 54$, $P = 0.071$), and Black-throated Huet-huets showed a similar abundance in both plot types ($U = 77$, $P = 0.75$; Fig. 1).

Maximum abundance of birds was significantly greater in high-bamboo plots than in low-bamboo plots ($U = 36.5$, $P = 0.036$; Fig. 2A). Species richness was also significantly greater in high-bamboo plots in three of the four patches ($U = 16.0$, $P = 0.024$; Fig. 2B). The most degraded forest (F4) was treated separately for species-richness comparisons because two species were absent despite the presence of dense bamboo stands.

In the 12 plots where vegetation variables were measured, understory bird abundance was significantly correlated with total understory cover (Pearson's $r^2 = 0.34$, $P = 0.045$; Fig. 3A) and bamboo cover ($r^2 = 0.43$, $P = 0.021$; Fig. 3B), but was not correlated with other kinds of plant cover ($r^2 = 0.18$, $P = 0.17$). Bird-species richness was positively correlated with

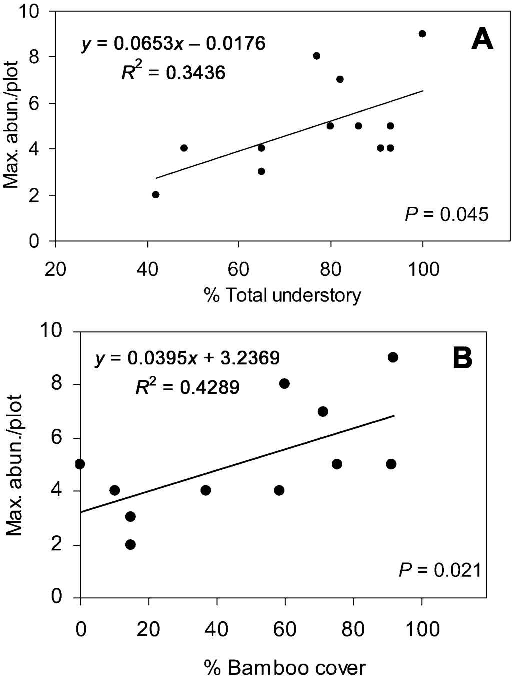

FIG. 3. Relationship between maximum abundance and (A) percentage of total understory cover and (B) percentage of bamboo cover.

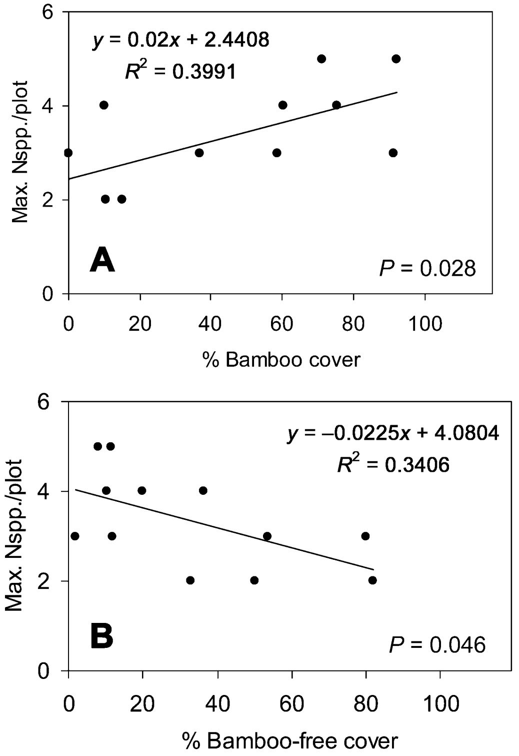

Fig. 4. Relationship between maximum richness and (A) percentage of bamboo cover and (B) percentage of bamboo-free understory.

bamboo cover ($r^2 = 0.40$, $P = 0.028$; Fig. 4A) and negatively correlated with other plant cover ($r^2 = 0.34$, $P = 0.046$; Fig. 4B) but unrelated to total cover in the understory ($r^2 = 0.10$, $P = 0.33$).

Bamboo as food resource.—Number of invertebrates per gram of understory showed no significant differences between forest patches (ANOVA: $F = 1.92$, df = 1 and 10, $P = 0.20$), so we pooled all plots with high bamboo and all plots with low bamboo from the different patches for the comparisons. No significant differences in the number of invertebrates per gram of understory were found between bamboo and other understory plants (ANOVA: $F = 2.56$, df = 1 and 10, $P = 0.15$). However, bamboo biomass per cubic meter was marginally higher than other understory biomass (1.4 ± 0.8 kg dry mass and 0.5 ± 0.3 kg, respectively; $t = -2.27$, df = 8, $P = 0.053$, $n = 5$). As a result, estimated number of invertebrates per plot was significantly higher in high-bamboo plots ($t = -5.501$, df = 10, $P < 0.001$; see Table 1).

Number of invertebrates in ground litter showed significant differences between forest patches (ANOVA: $F = 27.70$, df = 1 and 10, $P = 0.001$); therefore, comparisons between high- and low-bamboo plots were done separately for each patch. No significant differences were observed between high- and low-bamboo plots in either of the two forests (ANOVA: $F = 0.024$, df = 1 and 4, $P = 0.88$; $F = 1.923$, df 1 and 4, $P = 0.24$ for F1 and F3, respectively). The most common invertebrates in ground litter were ants, moths, and spiders.

Cover selection sites.–In experiments with nine different Chucao Tapaculos released from live traps, seven chose bamboo understory as the first perching place after release, one chose bamboo-free understory vegetation, and one flew straight ahead so fast that we were unable to record its first perching site. Although a marked preference for bamboo understory was observed, that preference did not yield a statistically significant difference with a sign test ($P = 0.07$).

Discussion

Importance of bamboo for understory birds.—Four of the five understory bird species were always more abundant in high-bamboo plots, supporting, in part, our initial hypothesis of a strong affinity between all those birds and bamboo understory. Many related understory species of tropical rainforest birds in the families Rhinocryptidae and Formicariidae are also strongly associated with understory bamboo thickets (Ridgely and Tudor 1994). Our findings are in accord with recent studies of McPherson (1999), who suggests that Ochre-flanked Tapaculos depend on bamboo cover, and with Sieving et al. (2000), who suggest that bamboo is an important predictor of bird use of forest corridors on Chiloé Island. Data of all bird species recorded in the bird surveys here ($n = 24$) also showed a significant higher bird-species abundance in high-bamboo plots (ANOVA: $F = 28.54$, df = 1 and 118, $P < 0.01$), but the importance of forest elements for those species is discussed in I. A. Díaz et al. (unpubl. data). In addition, many generalist species in those forests use understory for nesting, which reinforces the importance for the maintenance of a diverse forest avifauna; examples are the vulnerable Chilean Pigeon (*Columba araucana*), the Green-backed Firecrown (*Sephanoides galeritus*), the endemic Patagonian Tyrant (*Colorhamphus parvirostris*), and the White-crested Elaenia (*Elaenia albiceps*) (Johnson and Goodall 1967, Chesser and Marín 1994; S. Reid et al. pers. obs.). We propose that stands in a forest corresponding to the 50-m-radius sample plots in our study, having >75% of the area covered by bamboo, will help to ensure a significantly high understory bird abundance and species richness in similar forest patches in Chiloé Island. Although landscape configuration (fragmentation and isolation) must also be taken into account when predicting a species presence or abundance in a patch. We hypothesize that the absence of Ochre-flanked Tapaculos and Black-throated Huet-huets in F4 may be explained in part by the higher isolation of F4 to continuous forest, in addition to the higher disturbance because of past logging practices and fire.

Ecological role of native bamboo.–An innovative finding here was that bamboo habitat offers a greater potential food supply to invertebrate eaters because of the higher density of bamboo foliage. The higher invertebrate abundance in high-bamboo plots supports our first hypothesis, contributing to the observed preferences of understory bird species. Particularly, bamboo could be an important food supply for three leaf gleaners (Ochre-flanked and Magellanic tapaculos and Des Murs's Wiretails) that forage preferentially in branches of the understory. However, invertebrate availability on the ground did not differ between plots with high or low bamboo and may not affect birds that forage on the ground (Chucao Tapaculo and Blacked-throated Huet-huet). The observed similar abundance of Black-throated Huet-huet in both plot types means that there are other variables (not considered here) that explain habitat use in that species, such as patch size because of their large home ranges (Willson et al. 1994).

Concerning bamboo as a preferred escape cover (hypothesis 2), our preliminary exploration may support the preference of understory birds for bamboo cover (low number of birds tested could explain the lack of statistical significance). Bamboo cover would function as a potential refuge from predators because bamboo thickets are often very dense, with intricate branching that impedes the rapid movements of any organism taller than ~30 cm through the vegetation (S. Reid et al. pers. obs.). Reported predators for understory species in Chiloé Island are Rufous-legged Owl (*Strix rufipes*), Austral Pygmy-Owl (*Glaucidium nanum*), Bicolored Hawk (*Accipiter bicolor*), the native forest cat (*Oncifelis guiña*), the Darwin´s fox (*Pseudalopex fulvipes*), the mustelid quique (*Galictis cuja*), and possibly an introduced mustelid (*Mustela vison*) if its range continues to increase (Martínez and Jaksic 1996, Medina 1997, Sieving et al. 2000, Willson et al. 2001). All of those, except for the Austral Pygmy-Owl (20 cm; Johnson and Goodall 1967), are larger than the understory bird species and the spaces in the branching patterns of bamboo, so escaping into bamboo thickets could prevent the attack of those predators. Our preliminary result suggests a bamboo selection by Chucao Tapaculos, and bamboo is likely to serve as a more effective refuge from predators in comparison to other types of understory cover. Further studies should be conducted in the field to examine that hypothesis.

Management and conservation implications.–Habitat heterogeneity of forests, together with the size and connectivity of forest patches, is of paramount importance for the maintenance of a diverse forest avifauna (Freemark and Merriam 1986, Wiens 1989, Wenny et al. 1993, Faaborg et al. 1998, I. A. Díaz et al. unpubl. data). In Chile, most industrial logging practices tend to simplify forest structure, and the understory is usually burned or removed (Estades 1994, 1997; Donoso and Lara 1999). A dense understory, particularly bamboo thickets, has traditionally been considered a factor that significantly inhibits the establishment and growth of tree seedlings, and hence forest regeneration (Veblen 1982, Veblen et al. 1996); but a recent study in a *Nothofagus* forest in south-central Chile demonstrated that the removal of understory has no significant advantage to overstory wood production (Lusk and Ortega 2003). Therefore, it could be possible to maintain some level of understory cover in managed forests, enhancing understory bird conservation. Industrial management practices contrast with traditional small-scale, selective logging by landowners in Chiloé Island. In the former, extensive homogeneous stands with a sparse understory are generated; whereas in the second, understory heterogeneity is maintained and the development of bamboo cover may even be enhanced by removal of some canopy trees. According to our results, those two forms of management will have contrasting consequences for the persistence of understory birds in the regional landscape.

Southern temperate understory birds present several characteristics that make them very sensitive to land-cover changes: (1) they have poor flying abilities, (2) they are ground- and thicket-dwellers, (3) they are particularly sensitive to changes in habitat structure, and (4) they tend to decrease in abundance and species richness from large to small patches (Willson et al. 1994; Sieving et al. 1996, 2000; Cofré 1999; Estades and Temple 1999; Cornelius et al. 2000). Endangered forest pheasants (Phasianidae), which inhabit bamboo understory in southwestern China and share similar characteristics with the rhinocryptids in our study, are being successfully conserved in areas where "bamboo patches and corridors" are being set up, in the provinces of Shaanxi, Gansu, and Sichuan (Reid and Jien 1999). For southern temperate forest birds, bamboo density, corridor width, and presence of streams are the main predictors of bird use of corridors in Chiloé Island (Sieving et al. 2000). Our results suggest that bamboo not only functions as protective cover during travel but also plays an important role in determining the distribution and abundance of four of the five understory birds studied; it provides abundant food resources to invertebrate gleaners and may serve as a better refuge from predators. We propose that the maintenance of bamboo patch heterogeneity and the re-establishing of "bamboo corridors" in managed forests in Chiloé Island will help minimize the effect of logging on understory birds.

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