Ecological Applications, 9(2), 1999, pp. 573–585
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DECIDUOUS-FOREST BIRD COMMUNITIES IN A FRAGMENTED LANDSCAPE DOMINATED BY EXOTIC PINE PLANTATIONS

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Abstract. Impacts of habitat fragmentation on forest bird communities have often been studied in landscapes dominated by agriculture. The striking structural differences between forest fragments and the matrix have led most researchers to rely on island biogeographic theory to predict the distribution of bird species in fragmented forests. However, in some cases the vegetation surrounding fragments is not completely unsuitable for forest birds. Thus, a more general framework is needed to understand the effects of habitat fragmentation. The mosaic approach considers fragments as integrated parts of a complex landscape composed of patches of habitat of different qualities. In the coastal area of the Maule region in central Chile the remaining hualo (*Nothofagus glauca*) forests cover $<$10% of the landscape, are severely fragmented, and are imbedded in a matrix of exotic pine plantations. We compared the island and mosaic approaches as explanations for the distribution and abundance of forest birds. Variable circular plots were used to study the distribution of diurnal forest birds in hualo forest fragments and in the surrounding pine plantations. There was a negative relationship between the size of forest fragment and bird species richness per unit area. Fragmentation effects were mostly species-specific. A few large-sized bird species tended to be absent from the smaller fragments, while the presence or abundance of most birds showed no relationship with fragment size. The type of vegetation adjacent to forest fragments had a significant effect on the composition of the bird community inhabiting them. The abundance of most cavity-nesting species in pine plantations was related positively to the proximity of either the nearest native forest fragment or the nearest creek. On the other hand, the frequency of most open-nesting species in pine plantations was spatially unrelated to either forest fragments or creeks and depended mostly on the characteristics of the vegetation in the understory. Results support the use of the mosaic approach for the study of fragmentation on birds in forest-dominated landscapes.

Key words: bird communities; cavity-nesting birds; Chile; habitat fragmentation; island biogeographic model; landscape matrix; Nothofagus glauca; *open-nesting birds; pine plantations;* Pinus radiata.

INTRODUCTION

Habitat fragmentation, defined as the conversion of a large continuous patch of habitat into smaller, isolated or tenuously connected patches surrounded by a matrix of other habitat types (Wiens 1989), can affect avian communities in several ways. First, it reduces the area of the patches or fragments, decreasing their suitability for area-sensitive species that have large home ranges (Freemark and Merriam 1986, Robbins et al. 1989, Herkert 1994). Second, it isolates the patches from each other, affecting dispersal movements of isolation-sensitive species that become confined to each fragment (Temple 1991, Verboom et al. 1991, Villard et al. 1993). Third, it increases the proportion of edge habitat in patches, increasing negative interactions with species from adjacent habitats (Brittingham and Temple 1983, Wilcove 1985, Temple and Cary 1988). Finally, habitat fragmentation can affect species by changing their microclimate (Saunders et al. 1991) or decreasing prey abundance (Burke and Nol 1998). The consequences of fragmentation for bird populations vary, depending on factors such as the time since fragmentation, fragment size, distance between fragments, shape of the fragment (Saunders et al. 1991), or features of a species' life history (Hansen and Urban 1992). Responses of birds to landscape fragmentation tend to be individualistic and scale dependent (Jokimäki and Huhta 1996).

Many studies of the effects of forest fragmentation on bird communities have been conducted in fragments surrounded by agricultural lands, and island biogeographic theory (MacArthur and Wilson 1967) is usually invoked to explain patterns of species richness (Opdam 1991). However, in other situations, the surrounding habitat is not totally unsuitable for birds, and its characteristics determine how island-like the fragment will be (Pearson 1993, Hinsley et al. 1995, Stouffer and Bierregaard 1995). In such cases, habitat fragmentation creates a mosaic of habitat patches of different quality,

Manuscript received 22 August 1997; revised 20 April 1998; accepted 30 April 1998; final version received 29 May 1998.

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with forest fragments providing high quality habitat, and the matrix providing lower quality habitat (Barrett et al. 1994, Wiens 1994).

Avian communities in forested landscapes composed of high quality forest fragments embedded in a lower-quality forest matrix are not well studied. While McGarigal and McComb (1995) did not find significant negative effects of this type of landscape fragmentation on avian communities in the western USA, Enoksson et al. (1995) found that isolation of hardwood forest patches, within a coniferous forest landscape in Sweden, reduced the occurrence of some bird species with restricted dispersal capabilities.

During the last two centuries, the hualo (*Nothofagus glauca*) forests in central Chile have been extensively cleared and fragmented, both to provide land for agriculture and to produce timber and charcoal (San Martín and Donoso 1996). More recently, most of the landscape has been transformed into exotic pine (*Pinus radiata*) plantations, leaving only scattered fragments of natural forest embedded in a matrix of pine woodlands (Hormazábal and Benoit 1987, Gajardo 1994). Schlatter and Murúa (1992) and Muñoz-Pedreros et al. (1996) have identified the lack of nesting sites as a factor limiting the occurrence of breeding forest birds in pine plantations, and Estades (1994) reported fewer bird species in pine plantations than in the original *Nothofagus* forests in the Bío-bío region during winter. However, the effects of habitat fragmentation on bird communities in pine-dominated landscapes in central Chile are completely unknown. The only previous studies of avian communities in fragmented temperate forests of southern South America come from forest fragments embedded in agricultural landscapes (Willson et al. 1994, Sieving et al. 1996).

The dual aims of the present study are (1) to analyze the distributions of diurnal birds in fragments of hualo forest and in the pine matrix surrounding them in the Maule region, and (2) to provide landscape management guidelines that might help conserve native forest bird communities. Two alternative interpretations of the distribution and abundance of forest bird species in the landscape are analyzed.

First, we investigate how well the distribution and abundance of birds in fragments of hualo forest can be explained by simply considering the fragments as isolated ''islands'' of habitat. We would expect most birds to be confined to fragments and the presence and abundance of each bird species in a native forest fragment to depend on the size and isolation of the fragment.

Alternatively, we investigate how well the distribution and abundance of birds in fragments of hualo forest can be explained by explicitly considering the characteristics of the surrounding matrix. We would expect the composition of the bird community in fragments to be affected by the quality of habitat surrounding them. We also would expect the composition of the bird community in pine plantations to be affected by the proximity to native forest fragments.

METHODS

Study area

The study was conducted in the coastal Maule region of central Chile (Fig. 1). This region was originally covered by *N. glauca* deciduous forests (Gajardo 1994). The forests near the city of Constitución began to be cut in the early 1800s to provide wood for the ship building industry (San Martín and Donoso 1996). At present, the region holds some of the most extensive plantations of *P. radiata* in the country (Cerda et al. 1993). Relicts of hualo forest exist as small, isolated fragments in a pine-dominated landscape. Pine plantations cover ~76% of the landscape. Climate is mild, with an average minimum temperature for July (winter) of 5.9°C and an average maximum temperature for January (summer) of 22.7°C. Average annual rainfall is 881 mm (Santibáñez and Uribe 1993). Within this region, a 20 000-ha representative study area was selected (Fig. 1).

We conducted a detailed photointerpretation of the study area on 1:20 000 aerial photographs from 1994 and 1995. A minimum mapping area of one hectare was used. Land cover was mapped on 1:20 000 orthophotographs and digitized. Classification was verified using ground truthing. Approximately 95% of the study area was visited or observed using binoculars. Reclassifications, due to either incorrect photointerpretation or land cover change since 1994, were needed for ~10% of the landscape. Eight major vegetation types were mapped:

1) Mature pine plantations (8–25 yr old) covered 62.8% of the landscape. They averaged 537 trees/ha, with a mean height of 14 m, and a mean dbh of 19 cm. The understory was composed mainly of *N. glauca* and *Cryptocaria alba.*

2) Young pine plantations (3–6 yr old) covered 7.5% of the landscape. These open-canopy second-growth plantations had a mean height of 7.2 m, and a mean dbh of 9 cm. The understory was composed of shrub species and some coppices of *N. glauca.*

3) New pine plantations covered 6.0% of the landscape. Planted within the last three years, these plantations had trees less than 2 m tall. The understory was composed of shrub species, such as *Baccharis concava,* and debris left from previously harvested trees.

4) Unplanted pine clearcuts covered 3.4% of the landscape. Scrubby vegetation was composed of some young pines that germinated from residual seeds, mixed with coppices of native species, such as *N. glauca,* or *Lithraea caustica.*

5) Eucalyptus plantations covered 2.8% of the landscape. These were mostly young *Eucalyptus globulus* stands.

6) Open areas covered 5.6% of the landscape. They

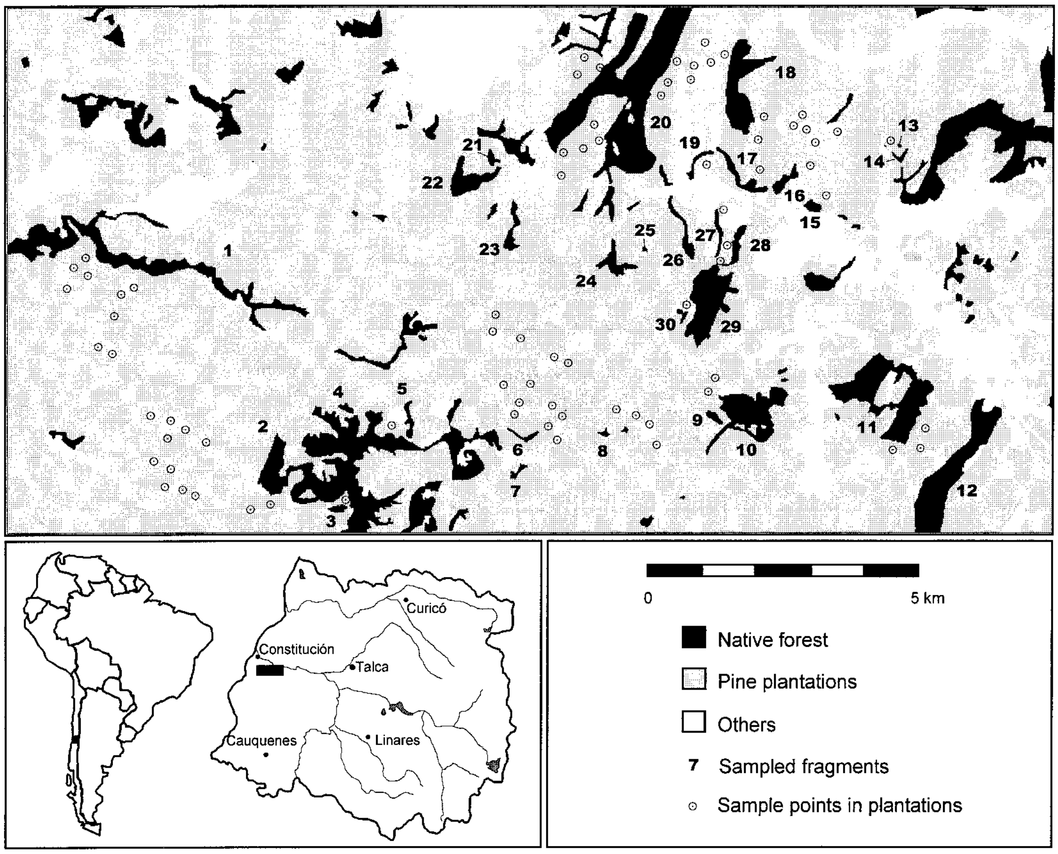

FIG. 1. Study area, in the Maule region of central Chile.

were dominated by nonnative grasslands, sparse scrubs, and agricultural fields.

7) Suburban areas covered 0.8% of the region. These included yards, gardens, lumberyards, sawmills, and houses.

8) Native forests covered 10.2% of the landscape. Most of these are second-growth *N. glauca* forests, which have been exploited for charcoal production. A few old-growth stands of *N. glauca* and *N. dombeyi* exist; most are on steep slopes near creeks. Their heights ranged from 6 to 21 m, with mean dbh from 4 to 36 cm.

Study design

Thirty native forest fragments were selected for the study (Fig. 1), covering a wide range of sizes (0.5–315 ha). Because it was impossible to find an adequate number of fragments with a homogeneous vegetation structure, we allowed structure to vary among the sampled fragments, but we explicitly considered its effects in our statistical analyses. For this purpose, we assigned more sample plots to larger and more heterogeneous fragments. Sixty-five sample plots were distributed among the forest fragments, resulting in a mean of one sample plot for every 16.1 ha of native forest. Fig. 2A shows the size distribution of the sampled fragments in relation to the available native forest patches.

Eighty-five sample plots were established in the pine plantations (Fig. 1). Plots covered proportionally the entire range of plantation ages and the entire range of distances from native forests (Fig. 2B). Plots also varied in their understory composition and structure.

Finally, we established 10 sample plots in open areas (vegetation type #6) adjacent to native forest fragments, because we were interested in knowing the response of forest birds to an abrupt edge. The location of these plots ranged from 50–500 m from the nearest forest stand.

The bird communities

Bird counts were conducted from mid-September to early November 1996 (austral spring) by four observers. At every sample plot, we used the variable circular-plot method (Buckland 1987) to estimate bird density. The maximum observation radius was 50 m, and each count lasted 5 min. Observations were conducted between 800 and 1200 on nonrainy days. All birds seen or heard within the maximum radius were recorded, and their distance from the plot's center was estimated in 10-m increments. Birds flying over a plot were not

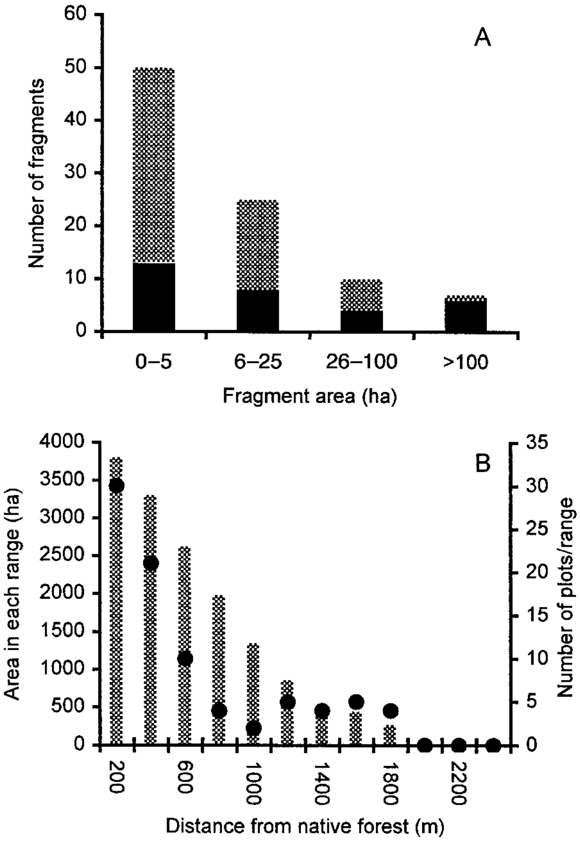

FIG. 2. (A) Number of sampled forest fragments (black), in relation to the available fragments (shaded) in four size classes. (B) Relationship between the area of pine plantations in 200-m increments from the nearest native forest fragment (bars) and the number of plots assigned to each (circles).

recorded unless they were somehow using the vegetation below them (e.g., swallows hunting insects just above the canopy). All points were visited four times, once by every member of the censussing team, at 6–10 d intervals. During a visit, the same observer conducted two 5-min counts, separated by a 10-min period. We followed this procedure in order to maximize our time spent in the sample plots in relation to the time traveling between plots.

Detectability curves were estimated for individual species in each vegetation type (native forests, pine plantations, and open areas). For census plots in forests and plantations, we compared detectabilities, in relation to the density of foliage, in the 0.31–2.0 m vegetation layer (which interferes with visibility). No such comparison was done for the 10 plots in the open areas. Within each of three categories of vegetation density (sparse, medium, and dense), we pooled data for every point and every replicate. The total frequency of observations at every 10-m increment was divided by the annular area encompassed by that increment and then divided by the maximum frequency in order to give values between 0 and 1. Detectability was assumed equal to one at the center of the plot. Finally, data were fitted to a hazard rate model curve (Buckland et al. 1993). The detectability function was then used to correct the observed densities following Buckland et al. (1993). Only models with $R^2 > 0.75$ were used to adjust detections for vegetation effects; otherwise, detectability was assumed to be uniform across the entire plot. Fig. 3 shows an example of a bird species whose detectability curves could be calculated and of one whose detectability function was assumed to be uniform.

Bird species richness was calculated as the total number of species recorded in each plot during the eight 5-min counts. Although nesting was not formally assessed in this study, we recorded all breeding activities and signs observed during the 80 min (20 × 4 visits) spent in every plot.

Habitat description

On every census plot, we characterized the vegetation structure and composition. For trees, we estimated total canopy height, basal area, mean dbh, and number of stems per ha using a relascope. To estimate plant species composition, we divided the 50-m radius plots in four quadrants, in each of which we estimated foliage cover in four layers (0–0.3 m, 0.31–2.0 m, 2.01–6 m, and >6 m). Foliage volume was calculated as the sum of the coverage of every layer times its height in meters. We described the percentage contribution of individual plant species to the foliage volume based on the sum of their (visual) frequency in each layer times

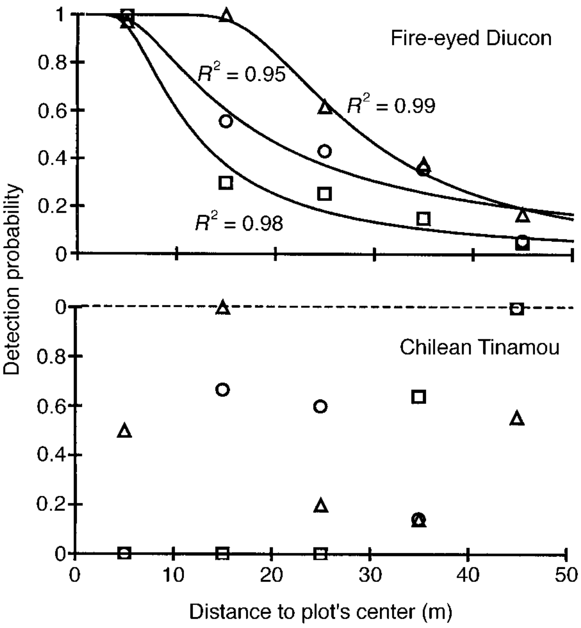

FIG. 3. Detectability functions for two bird species in pine plantations, in relation to three different levels of amount of vegetation in the understory: low (△), medium (○), and high (□). The dashed line represents a uniform detectability assumed throughout census plot.

the layer's foliage volume. Finally, we assigned to the plot the average value of all variables in the four quadrants.

Landscape analysis

Using a geographic information system (IDRISI; Eastman 1992) we calculated context variables for the sampled plots and fragments. For the plots located in native fragments, we calculated the total length of creeks in a 100-m radius around the center of each sample plot and the linear distance from each plot's center to the nearest creek. We included the effect of proximity to creeks because we suspected that the narrow strips of riparian vegetation that might have not been detected in our photointerpretation might be important for birds. For each native forest fragment, we calculated its total area. In order to account for the effect of the neighboring vegetation on birds in fragments, we calculated the area covered by each of the eight defined vegetation types within a 100-m buffer area surrounding the fragment. The width of the buffer area represents a reasonable home range diameter for most of the studied birds. The distance to the nearest native forest fragment and to the nearest native forest fragment larger then 50 ha were computed for every fragment, as an indirect estimate of isolation.

For the plots located in pine plantations, the following variables were measured: the total length of creeks in a 100-m radius around the center of each sample plot, the linear distance to the nearest native forest fragment, linear distance to the nearest native fragment larger than 5 ha, linear distance to the nearest native forest fragment larger than 50 ha, and linear distance from each plot's center to the nearest creek.

For the plots located in open areas, the only variable calculated was the linear distance to nearest native forest because we were interested on knowing how far forest birds would move into these areas.

Data analysis

Before performing analyses, all proportion variables were transformed by calculating the arcsin squared root (Zar 1984). Density data were transformed using the log(density + 1) to correct for heteroscedasticity. Bird species richness was expressed as the logarithm of the number of species. For species present in >2/3 of the sample units, we used multiple linear regression to detect fragmentation effects on the species density. First, we conducted a stepwise linear regression to analyze the effect of within-plot habitat variables on each of the bird variables. For this purpose, we included all structural variables and the abundance of the most common plant species (13 species). A variable was allowed to enter the model when $P \leq 0.1$. To avoid overfitting, a cross validation was performed using several subsets of the independent variables selected by the stepwise procedure. This was followed by selecting the model with the smallest sum of squares of predicted residual errors (PRESS statistic; Myers 1990). Then, we used the residuals of the latter and fitted them to a linear model, using the context data as independent variables, to see if there was any improvement in the predictions. For the analyses in forest fragments, we used the average of the values of all the plots within a fragment ($N = 30$). For bird species present in <2/3 of the sample units, a logistic multiple regression (Hosmer and Lemeshow 1989) was performed to detect any habitat or context effects on species presence/absence in a plot. We followed the same procedure as in the analysis of density data; but, instead of using the residuals of the within-plot vegetation model, we forced the selected predictors to stay in the model, while testing the additional contribution of context variables. For the analysis of data in forest fragments, we used all 65 plots in order to avoid the effect of uneven sampling effort in fragments of different sizes. However, we acknowledge that our choice may cause some pseudoreplication problems (Hurlbert 1984), and we interpret these results cautiously. Species present in <5 plots were not analyzed for habitat effects.

RESULTS

A total of 43 diurnal bird species was recorded in the study area (Table 1). All but three species are residents. *Patagona gigas* and *Elaenia albiceps* are tropical migrants that breed in the study area. *Colorhamphus parvirostris* migrates southwards during the spring; by the time of the study, most individuals had left. Population densities varied significantly among habitats for most species (Table 1). The total number of birds/ha was significantly higher in open areas and native fragments than in pine plantations (Tukey's hsd, $P < 0.0001$). Bird species richness was higher (Tukey's hsd, $P < 0.0001$) in open areas than in any other habitat (Table 1).

Birds in native forest fragments

Vegetation structure and composition.—Within-plot habitat variables explained much of the variance in most bird variables (Table 2).

Fragment size.—Bird species richness in a plot was significantly higher ($P < 0.05$) in smaller fragments than in larger fragments. The importance of log(fragment size) as predictor of species richness decreased when including the effect of creeks, but still remained weakly significant ($P < 0.1$; Table 2). *Asthenes humicola* and *Scytalopus magellanicus* showed a weak ($P < 0.1$) negative association with fragment size (Table 2). *Nothoprocta perdicaria* was the only species showing a significant positive relationship between density and forest fragment area (Table 2). *Enicognathus ferrugineus* and *Campephilus magellanicus* were recorded only a few times during the entire study and, therefore, were not analyzed formally. However, almost all the individuals we observed were found in the largest forest fragment.

TABLE 1. Bird community composition in different habitats near Constitución, Chile.

Species	Diet†	Nest‡	Mean number of birds per ha in the indicated habitats				
			Open areas (N = 10)	New pine (N = 5)	Young pine (N = 13)	Mature pine (N = 67)	Native forest (N = 65)
Nothoprocta perdicaria (Chilean Tinamou)	I(H)g	Og	0.6*a*	0.3*b*	0.2*b*	0.1*b*	0.1*b*
Vanellus chilensis (Southern Lapwing)	I(C)g	Og	0.1*a*	0*b*	0*b*	0*b*	0*b*
Cathartes aura (Turkey Vulture)	Cg	Oc	0*a*	0*a*	0*a*	0*a*	+*a*
Buteo polyosoma (Red-backed Hawk)	Cg(a)	Ot	0*a*	0*a*	+*a*	+*a*	+*a*
Milvago chimango (Chimango Caracara)	C(I)g	Ot	+*a*	0*a*	+*a*	0.1*a*	0.1*a*
Enicognathus ferrugineus (Austral Parakeet)	Gf(g)	Ct	0*a*	0*a*	0*a*	+*a*	+*a*
Callipepla californica (California Quail)	Gg	Og	0.2*a*	0.1*ab*	+*b*	+*b*	+*b*
Zenaida auriculata (Eared Dove)	Gg	Ots	0.9*a*	0.1*b*	+*b*	+*b*	+*b*
Columba araucana (Chilean Pigeon)	F(G)f(g)	Ot	0*a*	0*a*	0*a*	+*a*	+*a*
Caprimulgus longirostris (Band-winged Nightjar)	Ia	Og	0*a*	+*a*	0*a*	0*a*	+*a*
Sephanoides galeritus (Green-backed Firecrown)	N(I)f(a)	Os	0.1*b*	0.3*b*	0.8*b*	1.6*b*	3.0*a*
Patagona gigas (Giant Hummingbird)	N(I)f(a)	Os	+*a*	+*a*	0*a*	+*a*	+*a*
Picoides lignarius (Striped Woodpecker)	Is	Ct	+*b*	0*b*	+*b*	+*b*	0.1*a*
Colaptes pitius (Chilean Flicker)	Is(g)	Ct	0*a*	+*a*	+*a*	+*a*	+*a*
Campephilus magellanicus (Magellanic Woodpecker)	Is	Ct	0*a*	0*a*	0*a*	+*a*	+*a*
Aphrastura spinicauda (Thorn-tailed Rayadito)	I(F)f(s)	Ct	0.2*b*	0*b*	0.3*b*	0.4*b*	5.0*a*
Asthenes humicola (Dusky-tailed Canastero)	If	Sst	0.2*a*	0.1*ab*	0*b*	+*b*	0.1*ab*
Pygarrichas albogularis (White-throated Treerunner)	Is	Ct	0.1*b*	+*b*	0.1*b*	0.1*b*	0.8*a*
Sylviortorhynchus desmursii (Des Mur's Wiretail)	If	Os	+*a*	0.1*a*	0.1*a*	0.1*a*	0.1*a*
Cinclodes oustaleti (Gray-flanked Cinclodes)	Ig(w)	Og	0.4*a*	0*b*	0*b*	0*b*	+*b*
Leptasthenura aegithaloides (Plain-mantled Tit-Spinetail)	If	CSts	0.1*a*	+*bc*	0.1*ab*	+*c*	+*c*
Scytalopus magellanicus (Andean Tapaculo)	I(G)g(f)	Cg	0.2*a*	0.1*a*	0.1*a*	0.6*a*	0.5*a*
Pteroptochos castaneus (Chestnut-throated Huet-huet)	I(G)g	Cg	0*b*	0*b*	0*b*	+*b*	0.1*a*
Eugralla paradoxa (Ochre-flanked Tapaculo)	I(G)g	Cg	0.2*a*	0.3*a*	0.3*a*	1.0*a*	0.5*a*
Anairetes parulus (Tufted Tit-Tyrant)	I(F)f	Os	1.1*b*	0.4*b*	0.7*b*	1.3*b*	2.9*a*
Elaenia albiceps (White-crested Elaenia)	I(F)f(a)	Ots	0.2*c*	0.8*bc*	1.2*bc*	2.9*b*	7.1*a*
Pyrope pyrope (Fire-eyed Diucon)	I(F)a(f)	Os	1.9*a*	1.1*ab*	2.4*a*	1.5*a*	0.6*b*
Agriornis livida (Great Shrike-Tyrant)	Ia(f)	Os	0*a*	0*a*	+*a*	0*a*	+*a*
Colorhamphus parvirostris (Patagonian Tyrant)	If(a)	Os	0*a*	0*a*	0*a*	+*a*	+*a*
Tachycineta leucopyga (Chilean Swallow)	Ia	Ct	1.3*a*	1.2*ab*	0.3*ab*	0.2*b*	0.7*ab*
Troglodytes aedon (House Wren)	If	CSts	1.2*a*	1.4*a*	1.8*a*	2.1*a*	2.2*a*
Turdus falklandii (Austral Thrush)	F(I)g(f)	Ots	0.4*a*	0.2*a*	0.2*a*	0.3*a*	0.4*a*
Mimus thenca (Chilean Mockingbird)	F(I)g(f)	Os	1.7*a*	+*b*	0*b*	0*b*	0*b*
Phytotoma rara (Rufous-tailed Plantcutter)	H(F)f	Os	+*a*	0*a*	0*a*	0*a*	+*a*
Curaeus curaeus (Austral Blackbird)	I(H)g(f)	Os	1.6*a*	0.7*bc*	1.0*ab*	0.8*b*	0.4*c*
Sturnella loyca (Long-tailed Meadowlark)	I(G)g	Og	1.5*a*	0.5*b*	0.3*b*	+*b*	0.1*b*
Molothrus bonariensis (Shiny Cowbird)	I(G)g	P	0.3*a*	0*b*	0*b*	0*b*	0*b*
Zonotrichia capensis (Rufous-collared Sparrow)	G(I)g(s)	Osg	3.1*a*	2.4*a*	2.4*a*	1.0*b*	0.6*c*
Sicalis luteola (Yellow Grassland Sierra-Finch)	Gg	Og	1.5*a*	0.1*b*	0.1*b*	+*b*	*b*
Carduelis barbatus (Black-chinned Siskin)	Gg(f)	Osg	5.5*a*	1.5*b*	1.6*b*	1.0*b*	0.6*b*
Diuca diuca (Common Diuca-Finch)	Gg	Osg	5.1*a*	0.6*c*	2.3*b*	0.6*c*	0.3*c*
Phrygilus alaudinus (Band-tailed Sierra-Finch)	Gg	Og	0.9*a*	+*b*	+*b*	0*b*	0*b*
Phrygilus patagonicus (Patagonian Sierra-Finch)	G(H)g(f)	Ots	0.4*a*	0.3*a*	0.1*a*	0.6*a*	0.6*a*
All species			31.0*a*	12.6*b*	16.1*b*	16.5*b*	26.9*a*
Species richness			16.4*a*	12.6*b*	11.9*b*	10.8*b*	11.7*b*

Notes: For a row, values with the same letter are not significantly different ($P > 0.05$, Tukey's hsd). A plus (+) symbol indicates that mean density <0.05 individuals/ha.

† C, carnivores; F, frugivores; G, granivores; H, herbivores; I, insectivores; N, nectarivores; a, air; f, foliage; g, ground; s, stems; w, water. Secondary diet or substrate is given in parenthesis. (From Estades 1997*a*.)

‡ C, cavity; O, open nest; P, brood parasite; S, closed structure; c, cliffs; g, ground; s, shrubs; t, trees.

Isolation.—No clear effects of isolation on bird variables were observed. After considering vegetation effects on bird presence or abundance, the distance to other fragments turned out to be slightly significant only in the case of *Sephanoides galeritus* (Table 2), which tended to be more abundant in isolated plots ($P < 0.1$).

Vegetation surrounding fragments.—The amount of specific habitat types within the buffer area significantly improved the amount of variance in density or presence explained for many bird species (Table 2). The presence of some, mainly open-land, species, such as *Curaeus curaeus* and *Sturnella loyca* was related positively with the presence of open areas surrounding fragments ($P < 0.1$–0.05, Table 2). The abundance of *Zonotrichia capensis,* the most common garden bird species in Chile, was positively associated ($P < 0.05$) with the presence of suburban habitat near the fragments.

Distance to creeks.—Both bird species richness and total bird density were positively associated ($P < 0.01$ and $P < 0.001$, respectively) with proximity to creeks

TABLE 2. Habitat and landscape effects on bird species richness and abundance in native forest fragments.

	Effects of indicated factors on bird variables		
Bird variables	Model including within-plot vegetation	Additional effect of fragmentation and context variables‡	Model including within-plot vegetation, fragmentation and context variables
Bird species richness	0.23 (0.12)*	(−)LA,† Crk**	0.52 (0.09)***
Density of all birds	0.58 (0.25)***	Crk***	0.77 (0.19)***
Density (log[individuals/ha + 1])			
Sephanoides galeritus	0.36 (0.71)***	(−)Unp,* Iso†	0.46 (0.65)***
Aphrastura spinicauda	0.59 (0.72)***	···	···
Pygarrichas albogularis	0.43 (0.33)***	···	···
Scytalopus magellanicus	0.15 (0.34)*	(−)LA†	0.20 (0.33)*
Anairetes parulus	0.12 (0.52)*	···	···
Elaenia albiceps	0.21 (0.48)**	(−)Sub**	0.43 (0.41)***
Pyrope pyrope	0.61 (0.16)***	···	···
Troglodytes aedon	0.51 (0.41)***	(−)Open**	0.61 (0.37)***
Turdus falklandii	0.49 (0.25)***	Ypp,* Crk**	0.66 (0.20)***
Carduelis barbatus	0.38 (0.26)**	(−)Unp†	0.42 (0.24)**
Zonotrichia capensis	0.20 (0.27)*	Sub*	0.33 (0.24)**
Presence/absence			
Nothoprocta perdicaria	0.08*	LA†	0.12*
Picoides lignarius	0.27***	···	···
Asthenes humicola	0.27***	(−)LA†	0.35***
Pteroptochos castaneus	0.13***	(−)Ypp†	0.17***
Eugralla paradoxa	···	Unp,* (−)Euc,* Crk*	0.13**
Tachycineta leucopyga	0.15**	···	···
Curaeus curaeus	0.17***	Open*	0.21***
Sturnella loyca	0.08*	Open†	0.13*
Carduelis barbatus	0.07*	···	···
Phrygilus patagonicus	···	(−)Open**	0.10**

Notes: Numerical entries for bird species richness, density of all birds, and density of individual bird species are adjusted R^2 (1 SE). Numerical entries for presence/absence are McFadden's ρ^2. Richness and density were estimated using multiple linear regression ($N = 30$). Probability of the species being present in a plot was estimated using multiple logistic regression ($N = 65$).

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

† Statistical significance: $P < 0.1$.

‡ Effect indicated: variables as predictors of the residuals of the within-plot vegetation model. LA, log(fragment area); Crk, proximity to creeks; Iso, isolation, i.e., the distance to nearest 50-ha forest fragment. The following variables represent the amount of vegetation of a given type present in the 100-m buffer area surrounding forest fragments: Unp, unplanted clearcuts; Sub, suburban areas; Ypp, young pine plantations; Open, open areas; Euc, *Eucalyptus* plantations. Correlations are positive unless a negative sign is shown in parenthesis.

(Table 2). Among individual species, only *Turdus falklandii* and *Eugralla paradoxa* were positively related ($P < 0.05$ and $P < 0.01$, respectively) to proximity to creeks (Table 2). No negative effects of creeks were observed (Table 2).

Birds in pine plantations

Vegetation structure and composition.—Most bird variables were explained significantly by vegetation structure and composition within sample plots (Table 3). Total bird density was associated strongly with mean dbh (Fig. 4).

Distance to native forest.—Total bird density increased significantly with distance to native forests (Fig. 4). Bird species richness was not explained by distance to native fragments ($P > 0.1$; Table 3). Densities of cavity-nesting species declined significantly ($P < 0.05$) as the distance to native forests increased (Fig. 5A), although, individually, only *Tachycineta leucopyga* showed a weak negative relationship between the distance to the nearest forest fragment and the likelihood of being present in a plot ($P < 0.1$, Table 3). The relationship between the density of *Troglodytes aedon* and the distance to native forest fragments was negative close to fragments and then positive far away from them (Table 3). Finally, *Sephanoides galeritus* was significantly ($P < 0.05$) more likely to be present far from the native forest fragments (Table 3).

Distance to creeks.—The presence of creeks explained a significant part of the variance in many of the analyzed bird variables (Table 3). Bird species richness and total density of birds were related positively with proximity to creeks ($P < 0.0001$ and $P < 0.05$, respectively), after considering local vegetation effects. Densities of several bird species showed a positive association with creeks (Fig. 5B, Table 3).

Birds in open areas

Distance to native forest.—The probability of some cavity-nesting species, such as *Tachycineta leucopyga,*

TABLE 3. Habitat and landscape effects on bird species in pine plantations.

	Effects of indicated factors on bird variables		
Bird variable	Model including within-plot vegetation	Additional effect of context variables‡	Model including within-plot vegetation and context variables
Bird species richness	0.25 (0.18)***	(−)DC***	0.40 (0.16)***
Density of all birds	0.32 (0.32)***	(−)DC*	0.36 (0.31)***
Density (log[individuals/ha + 1])			
Anairetes parulus	0.11 (0.52)***	(−)DC†	0.14 (0.51)***
Elaenia albiceps	0.56 (0.33)***	···	···
Pyrope pyrope	0.16 (0.53)***	···	···
Troglodytes aedon	0.16 (0.41)***	(−)DN,*** DN*	0.23 (0.39)***
Zonotrichia capensis	0.29 (0.38)***	···	···
Carduelis barbatus	0.15 (0.47)***	···	···
Presence/absence			
Nothoprocta perdicaria	0.14***	···	···
Milvago chimango	0.07*	···	···
Sephanoides galeritus	0.05***	DN*	0.09***
Picoides lignarius	···	(−)LDC*	0.15***
Aphrastura spinicauda	···	(−)LDC***	0.20***
Asthenes humicola	0.27*	···	···
Pygarrichas albogularis	0.05*	(−)LDC*	0.10***
Leptasthenura aegithaloides	0.32***	···	···
Pteroptochos castaneus	0.33***	···	···
Eugralla paradoxa	0.04*	(−)DC*	0.12***
Tachycineta leucopyga	···	(−)LDN†	0.03†
Turdus falklandii	0.03*	(−)LDC†	0.06*
Curaeus curaeus	0.17***	···	···
Sturnella loyca	0.39***	(−)DC*	0.48***
Sicalis luteola	0.34***	···	···
Carduelis barbatus	0.14***	···	···
Phrygilus patagonicus	0.08***	···	···

Notes: Numerical entries for bird species richness, density of all birds, and density of individual bird species are adjusted R^2 (1 SE). Numerical entries for presence/absence are McFadden's ρ^2. Richness and density were estimated using multiple linear regression ($N = 85$). Probability of the species being present in a plot was estimated using multiple logistic regression ($N = 85$).

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

† Statistical significance: $P < 0.1$.

‡ Effect indicated: variables as predictors of the residuals of the within-plot vegetation model. DN, distance to native forest; LDN, log(distance to native forest); DC, distance to creeks; LDC, log(distance to creeks).

Aphrastura spinicauda, and *Pygarrichas albogularis,* being present in open areas declined significantly with the distance to the adjacent native forests ($P < 0.1$–0.01, logistic regression). The latter two species were never observed at distances >60 m from the native fragments. The probability of some open-area species, such as *Mimus thenca, Sturnella loyca, Phrygilus alaudinus,* and *Sicalis luteola,* being present in the plots increased with distance to forest ($P < 0.05$–0.0001, logistic regression).

Breeding activity

The average number of breeding signs recorded per sample plot (active nests, old nests, birds carrying nest materials, and the presence of fledglings) was significantly higher (Mann–Whitney U test, $P = 0.003$) in native forests ($N = 33$) than in pine plantations ($N = 15$). Cavity-nesting species, such as *Aphrastura spinicauda, Pygarrichas albogularis,* and *Tachycineta leucopyga,* were among the most frequently observed breeding birds in native forests. On the other hand, in the pine plantations, all observed nests were located in the native understory vegetation. *Pyrope pyrope, Elaenia albiceps, Anairetes parulus,* and *Troglodytes aedon* were the most commonly observed breeders.

DISCUSSION

Patterns of habitat use by birds

Fragmentation effects.—Island biogeographic theory (MacArthur and Wilson 1967) predicts that small islands (or habitat fragments) will have fewer species per unit area than larger islands (or habitat fragments). However, in the present study, the mean number of bird species per sample plot was slightly higher in smaller fragments. This pattern might be explained by a relatively higher number of nonforest or edge species in smaller fragments (Loman and von Schantz 1991, Bellamy et al. 1996), but this does not seem to be the case on our study area. The abundance of edge and open area species, such as *Zonotrichia capensis* and *Sturnella loyca,* showed no significant relationship with the

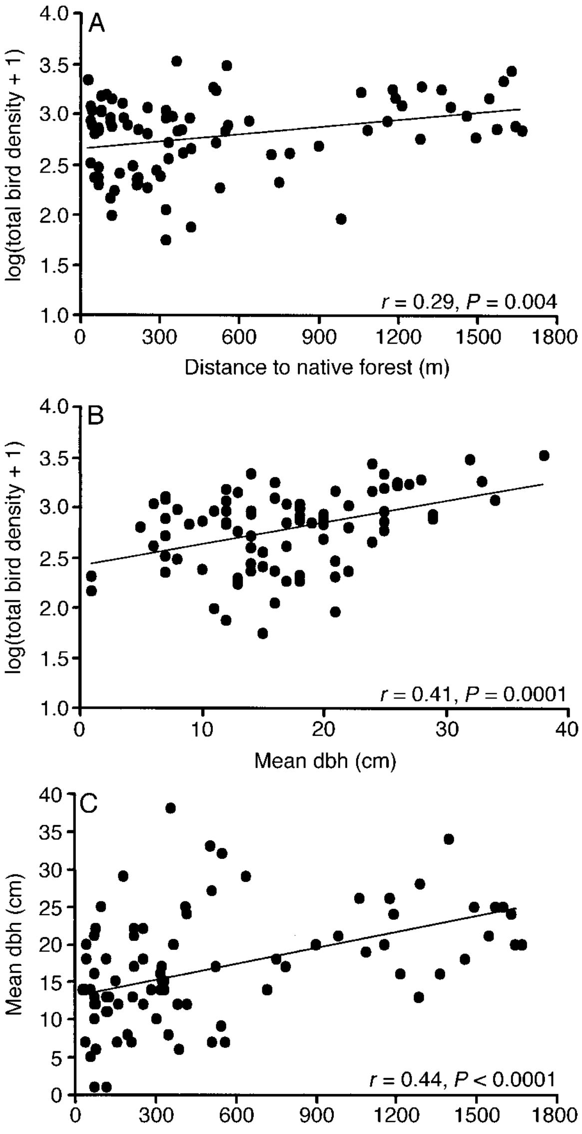

FIG. 4. (A) Relationship between the mean pine dbh (diameter at breast height) and the distance to the nearest forest fragment. (B) Relationship between the logarithm of the total bird density in pine plantations and the mean pine dbh. (C) Relationship between the logarithm of the total bird density in pine plantations and the distance to the nearest forest fragment.

size of the fragments. However, the same two species were significantly more abundant in fragments that were adjacent to open and suburban areas, regardless of their size, indicating that the surrounding matrix affects the composition of the fragment's avifauna. We suspect that most forest birds were as likely to be found, and to be as abundant, in plots in small fragments as they were in plots in large fragments, due to the use of surrounding habitats (Andrén 1994). Bird species in *Nothofagus*-dominated communities have broad niches and wide distributions among habitats (Vuilleumier 1985). This preadaptation might allow bird species in hualo forests to cope with different types of habitats, such as pine plantations, more easily.

Despite the negative relationship between species richness and fragment area, some species were clearly area-sensitive. *Nothoprocta perdicaria, Enicognathus ferrugineus,* and *Campephilus magellanicus* were more likely to be found in large fragments. All these species are large birds (31–47 cm total length, Johnson 1967), which agrees with the prediction that large species are more area-sensitive (Turner 1996). *Nothoprocta perdicaria* showed this pattern, despite its even distribution among forested habitats (Table 1).

Loman and von Schantz (1991) argued that their failure to find a positive relationship between bird species richness and habitat fragment size in an agricultural landscape in Sweden might have been due to the fact that the fragments studied were very small (≤24 ha) and that most area-sensitive species might have already been eliminated from the study area. In our case, we recorded almost all the forest species likely to be found in the region, and, therefore, we assume that our results were not biased, because area-sensitive species were already missing.

Isolation of fragments, expressed as the distance to the nearest 50-ha fragment, did not have a negative effect on bird species richness in fragments as predicted

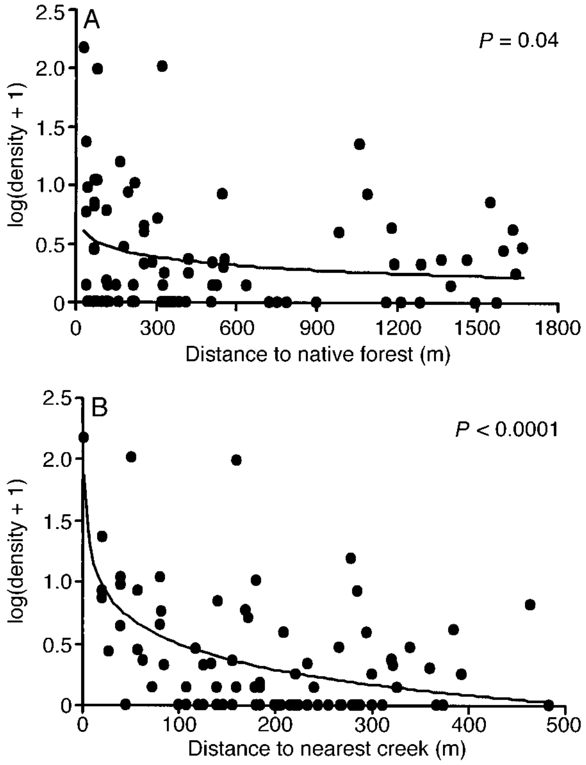

FIG. 5. Logarithm of the density of all cavity-nesting species in pine plantations, in relation to (A) the distance to the nearest forest fragment and (B) the distance to the nearest creek.

by the island biogeographic theory. The fact that the proximity to creeks enhanced both bird density and richness in fragments (after considering vegetation effects) suggests that creeks may be increasing connectivity of the landscape. In addition, because many bird species were actively using the matrix, isolation of forest fragments may not be important for them.

The effects of vegetation structure and composition on bird species abundance were strong (Table 2) and generally agree with the patterns found by Estades (1997*a*) in montane *Nothofagus* forests. The variation in vegetation features among and within fragments was reflected in a significant variation of the densities of some bird species between different plots, in different fragments, and within a fragment. Even though we controlled for vegetation effects, its high heterogeneity, along with the irregular shape of most of the studied fragments (Fig. 1) may have obscured, to some extent, the effects of fragmentation on the composition of the bird communities in the study area. However, the studied fragments are representative of the extensively altered landscape in the region (C. F. Estades and S. A. Temple, *personal observation*), and we are confident that our conclusions are conservative and should be useful for most managers dealing with similar situations.

Birds in pine plantations.—Forest birds in the study area clearly made use of the pine plantations. Average total bird densities in young and mature plantations (see Table 1) were well within the ranges reported for natural temperate forest communities in South and North America (Jaksic and Feinsinger 1991) and higher than densities reported for pine plantations in other parts of the world (e.g., Repenning and Labisky 1985, Parker et al. 1994). However, part of this difference may be due to the use of different censussing techniques, because not correcting for visibility tends to underestimate the densities. The number of bird species observed in pine plantations did not differ from the numbers recorded in native forests (although species composition was different), agreeing with observations conducted in New Zealand (Clout and Gaze 1984). Interestingly, the vegetation composition in Chile and New Zealand are quite similar, with the native forest being composed of trees in the genus *Nothofagus* and *Podocarpus,* among others, and the plantations composed mainly of *Pinus radiata.*

The total density of birds was significantly higher in plantations located far from forest fragments. This apparently surprising result is largely because the mean dbh in the pine plantations is correlated positively with the distance from native forests (Fig. 4C), and distance itself has no effect on bird community variables (Table 3). This finding disagrees with the results obtained by Curry (1991) in Australia, where both bird species richness and total bird density decreased with distance to native forest. The relationship between mean dbh and distance to native fragments might be explained by the pattern of afforestation that may have taken place in the study area during the last decades. The best lands were the first to be planted with pine, and, as the industry expanded, the less productive lands (located close to the remaining native vegetation) were converted into plantations.

The abundance of some forest bird species in pine plantations was strongly dependent on proximity to native vegetation. Almost all cavity-nesting species were more abundant close to either native forest fragments or creeks (Table 3; Fig. 5). Two different explanations for this pattern seem reasonable. First, the characteristics of the habitat in pine plantations close to the native fragments or the creeks could be more favorable for these species. Second, individual birds could be including native forest and creeks, as well as nearby plantations, into their home ranges. The first explanation is not supported by the data. There were no significant relationships between vegetation variables and distance to either creeks or native fragments. The only significant association was the positive relationship between dbh and distance to fragments (Fig. 4C), but mean dbh of pine was not a predictor of the density of any cavity-nesting species.

The second explanation seems more plausible to us. Although we did not assess individual bird movements, we have indirect evidence that at least some of the cavity-nesting birds observed in the pine plantations came from nearby native forests. For example, when counting birds in very small fragments, we observed that some individuals of *Aphrastura spinicauda* nesting in the fragment would leave and then return after some minutes, probably spending time in the surrounding pine plantations.

Whether forest bird species use riparian vegetation along creeks as breeding habitat or simply as travel corridors is a question that cannot be answered with our data. Most of the creeks found within the pine plantations have narrow strips of native vegetation that, in most cases, are only 2–3 m wide and undetectable on aerial photographs, because the pine canopy is often closed over them. Nevertheless, subtle differences in vegetation structure, plus the presence of some native trees and snags, seem to make these riparian strips attractive to many birds. Some cavity-nesting species were observed in pine plantations at distances as far as 1700 m from the nearest native forest fragment. These birds either might be breeding in nearby riparian vegetation, or they might be wandering nonbreeding individuals.

In contrast to their frequent use of pine plantations, forest birds make little use of open areas. Cavity-nesting species remained near native forests and only occasionally visited scattered trees in open areas. On the other hand, some understory species, such as *Scytalopus magellanicus* and *Eugralla paradoxa,* were found >400 m from forest in areas where scattered shrubby cover was available, agreeing with the results obtained by Sieving et al. (1996) in Southern Chile.

Native vegetation inside the pine plantations had a strong effect on the composition of the bird community. The amount of native vegetation in the understory was associated positively with the densities of many bird species, mostly insectivores that foraged and nested in this layer (data not presented, but see Estades 1997*b*). The pine canopy was less used than understory vegetation, and few birds were actually observed foraging in the pine foliage. *Carduelis barbatus* was observed feeding on new buds, and *Troglodytes aedon* and *Aphrastura spinicauda* were occasionally seen looking for insects in the lowest branches of the trees. Many birds, however, used the pines as singing posts and observation perches. These patterns coincide with the results of many studies that conclude that the presence of native vegetation inside pine plantations is one of the most important factors determining their use by birds (Dickson et al. 1984, Cruz 1988, Curry 1991, Estades 1994).

Island vs. mosaic approach.—Fragments of habitat have often been considered as islands, and management concerns have focused on improving features of the habitat patches based on island biogeographic theory. Thus, managers have been mostly concerned about the size and shape of fragments, the distance separating them, and corridors that connect them (Shafer 1990). The fact that the bird community composition in forest fragments varies in relation to the features of the surrounding matrix (Loman and von Schantz 1991, Andrén 1994, Hinsley et al. 1995, Bellamy et al. 1996, Jokimäki and Huhta 1996) provides an alternative framework for the management and conservation of bird populations in fragmented landscapes. This alternative view considers fragments to be integrated parts of a complex mosaic of different types of habitats (Wiens 1994). The potential relationships between the mosaic's patches imply that the management of any one of them might affect the characteristics of others.

The characteristics of the matrix surrounding *Nothofagus* forest fragments in Chile do impact the bird communities inhabiting them. Where the matrix has been managed for agriculture or cattle grazing, *Nothofagus* forest bird communities have shown a positive relationship between bird species richness and the size of fragments (Willson et al.1994). In the present study, where the matrix has mostly been managed for pine plantations, the trend was reversed.

The presence of pine plantations in the matrix may prevent the occurrence of some physical changes associated with fragmentation. The effects of solar radiation and wind, which are known to be very disruptive to the biota of some fragmented forests (Saunders et al. 1991), may in fact be negligible in our study site, because there is almost a continuous canopy cover. This continuous vegetation cover may also reduce some negative biological interactions associated with edges, like predation and brood parasitism. In fact, we did not observe a single individual of *Molothrus bonariensis,* the local brood parasite, either in pine plantations or in native forest fragments, and yet they were quite abundant in nearby open areas.

Adding information about the type of vegetation surrounding individual fragments contributed significantly to our ability to explain variation in the presence or abundance of several bird species (Table 2). The most consistent pattern was the positive effect of the presence of open or suburban types of habitats on the presence of open and shrubland species (Table 2).

Similarly, adding information on the proximity of native vegetation significantly improved the amount of variance explained for the abundance or presence of many bird species in pine plantations (Table 3).

Management implications

The type of management applied to pine plantations influences their suitability as habitat for birds. Plantations managed with high tree densities and no pruning, as those used exclusively for the pulp industry, usually have a poorly developed understory that supports a very depauperated avifauna (Estades 1994). Nevertheless, the plantations on our study area are managed for pulp and timber, usually being thinned and pruned at least twice during a rotation. This management facilitates the development of native vegetation in the understory, and it allows a significant number birds from the nearby forest fragments to forage in the plantations and occasionally to breed there.

The presence of sparse pine plantations in the matrix probably generates one of the best possible scenarios for forest birds in central Chile where native vegetation already covers $<10\%$ of the area. Pine plantations provide a ''soft edge'' (sensu Stamps et al. 1987) for forest fragments in contrast to the ''hard edges'' between forests and open areas. However, not all features of the pine–*Nothofagus* edge are beneficial for the fragments and the birds that inhabit them. We observed that pines are able to colonize the adjacent native forests and to outcompete the native vegetation, due to their higher growth rate. Thus, native forest fragments are actually shrinking, and all of the ones we studied already had some pines among the dominant trees in their canopy. Therefore, the preservation of remaining native forest fragments will not be achieved by a ''laissez-faire'' policy, but will require some active removal of encroaching pines.

Regardless of their size, all existing *Nothofagus* fragments in the coastal Maule region hold an important number of forest birds. They should be maintained, and the restoration of some additional areas encouraged. It is also important to conserve some large tracts of native forest if area-sensitive bird species, such as *Campephilus magellanicus* and *Enicognathus ferrugineus,* are to be preserved in the region. Ideal management of pine plantations should enhance the native understory vegetation, in order to facilitate their beneficial effects on the remaining native forests.

Although we do not have data to directly support the hypothesis that creeks are increasing the connectivity between fragments, riparian strips are a very influential feature of the landscape significantly affecting the composition of the bird community. They should be preserved and enhanced.

Armstrong et al. (1996), studying vascular plants, mammals and birds in South Africa, concluded that pine plantations surrounding native vegetation fragments should be considered ''inhospitable seas''. However, their study site encompassed only 800 ha of pine plantations, and they did find several native species inhabiting them. The disagreement between their conclusions and ours may in part be a scale-related phenomenon. Dias and Blondel (1996) hypothesized that local populations of birds might be better adapted to the most abundant habitat type. If this is true, it could affect the comparison of the results of studies conducted in landscapes, where the relative proportions of native forests and pine plantations differ significantly.

Although the bird distribution patterns observed in this study have lead us to draw conclusions, we cannot fully assess the impact of pine plantations on native birds until breeding productivity of the studied populations is formally studied. This remains as an immediate imperative.

ACKNOWLEDGMENTS

This study was funded in part by the Zoological Society of Milwaukee County. The School of Forest Sciences of the University of Chile provided the lodging and helped with the logistics. Forestal Celco, Forestal Copihue, and R. León kindly granted us permission to conduct research in their properties. During the duration of this study, C. F. Estades was partially supported by a Fulbright Scholarship and by an Eduardo Neale-Silva Memorial Scholarship at the University of Wisconsin–Madison. A. F. Gajardo, P. Higueras, and J. C. Silva helped with all the fieldwork. S. Hannon, N. E. Mathews, D. J. Mladenoff, F. K. A. Schmiegelow, and P. Stouffer made valuable comments on different versions of the manuscript. The publication of this article was made possible by a contribution from the Max MacGraw Wildlife Foundation.

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