Effects of Habitat Fragmentation on Bird Species in a Relict Temperate Forest in Semiarid Chile

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Abstract: *We analyzed the structure and composition of a bird assemblage in a fragmented relict temperate forest located in northcentral Chile (Fray Jorge National Park). In terms of species composition, the bird assemblage we found in Fray Jorge was more similar to southern temperate forest sites, located more than 1200 km south of Fray Jorge, than to localities found in nearby scrub habitats. The relict character and long-term isolation of the Fray Jorge forest provides a natural experiment with which to establish the potential long-term effects of fragmentation and isolation on southern Chilean temperate forests. Between May 1996 and March 1997, we conducted seasonal surveys of birds in six forest fragments, ranging in size from 0.5 to 22.5 ha, at Fray Jorge. The number of bird species at each forest fragment was positively correlated with fragment area during all seasons. The relict forest system had a steeper species-area slope than that reported for similar temperate-forest bird assemblages in forest fragments within Chiloé Island and for islands across the Chiloé Archipelago in southern Chile. In this regard, this bird fauna resembled a depauperate oceanic archipelago. This difference in area effects is likely a consequence of the minimization of rescue effects because of the absence of large source forest areas nearby and the long-term isolation of the system. In addition, the distribution of species among forest fragments in Fray Jorge was not random, showing a nested subset pattern. Thus, some species occur across all fragments, regardless of their area, and therefore are less affected by habitat fragmentation and less prone to local extinction. These results suggest that, for south-temperate forest birds, large fragments (or reserves) should afford better protection against extinction than small forest patches.*

Efectos de la Fragmentación del Hábitat en Especies de Aves en un Bosque Relicto Templado Semiárido de Chile

Resumen: *Analizamos la estructura y composición de un ensamblaje de aves de un bosque relicto templado localizado en el centro-norte de Chile (Parque Nacional Fray Jorge). Con relación a la composición de especies, el ensamblaje de aves de Fray Jorge fue más similar a sitios de bosque templado, ubicados a más de 1200 km al sur de Fray Jorge, que a localidades ubicadas en hábitats arbustivos cercanos. El carácter relicto y el aislamiento de largo plazo del bosque de Fray Jorge proveen un experimento natural para establecer las consecuencias a largo plazo de la fragmentación del bosque templado del sur de Chile. Entre mayo de 1996 y marzo de 1997, se llevaron a cabo conteos estacionales de las aves en seis fragmentos de bosque con tamaños de 0.5 - 22.5 ha. El número de aves en cada fragmento se correlacionó positivamente con el área de éstos durante todas las estaciones. En términos comparativos, el sistema de bosque relicto tuvo una pendiente más pronunciada para la relación especies-área que la reportada para ensamblajes de aves similares en fragmentos de bosques de la isla de Chiloé y para las islas del archipiélago de Chiloé en el sur de Chile. A este respecto, la fauna de aves en Fray Jorge es similar a la de un archipiélago oceánico empobrecido. Esta diferencia en los efectos del área es probablemente una consecuencia de la minimización de efectos de rescate debido a la ausencia de áreas-fuente grandes cercanas y debido al largo tiempo de aislamiento de éste sistema. También encontramos que la distribución de especies en los fragmentos del bosque de Fray Jorge no es aleatoria, mostrando un patrón característico de subconjuntos anidados. Esto implica que hay algunas especies que se encuentran distribuidas en todos los fragmentos, no importando su área y, por lo tanto, son menos*

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afectadas por la fragmentación del hábitat y menos susceptibles a la extinción local. Estos resultados sugieren que para las aves del bosque templado, los fragmentos (o reservas) de gran tamaño podrían proveer una mayor protección contra la extinción que los parches de tamaño pequeño.

Introduction

Fragmentation of habitats due to natural processes or more commonly to human perturbation is apparent and widespread in most landscapes around the world (e.g., Andrén 1994; Vitousek 1994; Meffe & Carroll 1997). The fragmentation of a previously continuous habitat entails habitat loss and an increase in isolation, which in turn usually trigger a cascade of biological effects such as edge effects, decreased colonization, increased mortality, and habitat degradation, causing an increase in extinction rate, loss of biological diversity (e.g., Wilcox & Murphy 1985; Saunders et al. 1991), and nonrandom patterns of species distribution across fragments (Patterson & Atmar 1986; Blake 1991; Cutler 1991; Soulé et al. 1992).

Major ecosystem types have already been reduced to fragments, and numerous species and genetically distinct populations have been lost in the process (Ehrlich & Wilson 1991; Wilson 1992). Analysis of a global database on human disturbance of natural habitats indicates that this type of disturbance is acute in temperate biomes in South America (Hannah et al. 1995). In southern South American temperate forests in particular, human encroachment, fire use, agriculture, and commercial logging have caused intense fragmentation and reduction of forest area (Armesto et al. 1994; Bustamante & Grez 1995; Lara et al. 1996). The loss and degradation of this forest ecosystem is even more dramatic if one considers its insular character, with high endemism and low species richness due to glaciation episodes (Vuilleumier 1985), and its inadequate protection in national parks and reserves (Armesto et al. 1998). From any viewpoint, this is an ecosystem with high priority for conservation, as has been recognized internationally (Armesto et al. 1992, 1998; Dinerstein et al. 1995). Little is known, however, about the effects of fragmentation in this system (Estades 1994; Willson et al. 1994; Sieving et al. 1996), which makes it difficult to predict its consequences for component species, especially in the face of nonlinearity in species' responses (Andrén 1994), non-equilibrium situations (Kellman et al. 1996), and time-lagged extinctions in response to habitat destruction or "extinction debt" (Tilman et al. 1994).

We analyzed the structure and composition of a bird assemblage in a fragmented forest located in Fray Jorge National Park in northcentral Chile. This is a relict temperate forest found in a fog-induced microclimate in a regional matrix where the predominant vegetation is semiarid scrub. The relict character and long-term isolation of this forest provide a natural experiment with which to assess the consequences of fragmentation in a system where propagule rain and rescue effects (e.g., Brown & Kodric-Brown 1977; Gotelli 1991) from nearby nonfragmented forests are minimal in comparison with those of fragmented systems located in southern Chile, where this forest type is still widespread. We hypothesize that the effects of fragmentation on the Fray Jorge forest have been strong, resulting in a depauperate bird fauna with a species-area slope more similar to that of an isolated oceanic archipelago than a mainland relaxing system. This should be a system that has already paid its extinction debt.

To assess whether it is valid to use the relict forest of Fray Jorge to infer the potential long-term consequences of fragmentation and isolation on bird species assemblages inhabiting southern-hemisphere temperate forests, we started our analysis with a biogeographical comparison of the Fray Jorge forest avifauna with that of (1) temperate forests located more than 1200 km south of our study site and (2) nearby semiarid and mediterranean sites. Subsequently, we analyzed the structure of the bird assemblage in the relict forest and evaluated extinction-driven patterns of assemblage structure.

Study Area

We conducted our study at the relict forest in the Fray Jorge National Park (lat 30°40′S, long 71°30′W), located 94 km south of Coquimbo, Chile (Fig. 1). The climate is mediterranean-arid, with dry, hot summers and cool winters (di Castri & Hajek 1976). Mean annual precipitation is 85 mm, falling mainly between May and September. The forest is restricted mostly to sea-facing slopes on top of the coastal mountain range (600 m elevation); it has a total area of 235.4 ha and is composed of several fragments ranging between 0.5 to approximately 45 ha in area. Dominant floral species are the trees *Aextoxicon punctatum*, *Drimys winteri*, and *Myrceugenia correifolia*; the evergreen shrubs *Luma chequen* and *Raphithamnus spinosus*; one prostrate species, *Griselinia scandens*; and several ferns in the genus *Hymnophylum* (Araya et al. 1992). The scrub matrix habitat surrounding fragments in the mountain range extends into the lowland area (200 m elevation), with an associated increase in cover of dominant species such as *Porlieria chilensis*, *Proustia pungens*, and *Adesmia bedwellii* (Muñoz & Pisano 1947). This xeric vegetation corre-

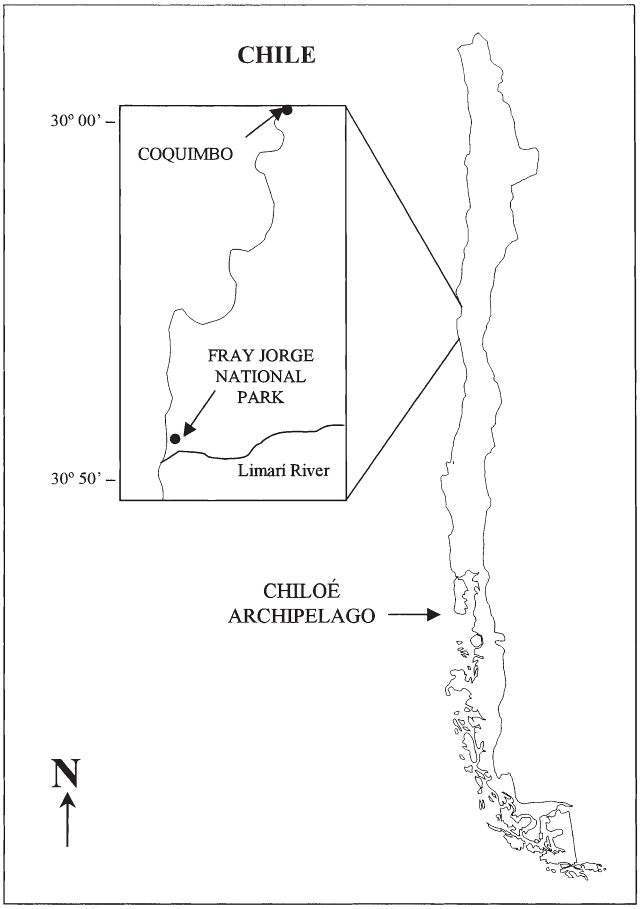

Figure 1. Study site in Fray Jorge National Park in northcentral Chile.

sponds to the Coastal Stepparian Matorral of Coquimbo (Gajardo 1993; Araya et al. 1992).

The floristic composition, relative abundance of tree species, and soil chemistry of the Fray Jorge forest closely resembles those of the Valdivian temperate forest currently distributed >1200 km south of Fray Jorge (Villagrán & Armesto 1980; Pérez & Villagrán 1985, 1994). Recent floristic and paleontological studies indicate that this relict forest was derived from a widely distributed flora (the mixed and subtropical flora of coastal Chile) that by the end of the Tertiary became increasingly isolated as a result of climatic changes (Villagrán & Armesto 1980; Troncoso et al. 1980; Hinojosa & Villagrán 1997; Villagrán & Hinojosa 1997). It became restricted to its present location, associated to the coastal mountain range, during the Quaternary (Troncoso et al. 1980; Villagrán & Hinojosa 1997).

Methods

At Fray Jorge we used aerial photographs (scale 1: 20000) taken in 1993 to select six forest fragments so as to obtain a wide range of fragment areas and to maximize the distance between them (to assure independence of counts), which ranged between 360 and 3130 m. Selection of sites was subject to accessibility and permission from the National Park Administration. Because these forest fragments were in a protected area, we expected minimal change in their size from 1993 to 1997. The fragment labels and size, respectively, were as follows: F1, 0.5 ha; F2, 0.6 ha; F3, 3 ha; F4, 5.9 ha; F5, 15.7 ha; F6, 22.5 ha.

We carried out bird surveys in six fragments and in the scrub matrix (in the mountain range and lowland area) from dawn to 1300 hours in May, August, December, and March, corresponding to austral autumn, winter, and spring of 1996 and summer of 1997, respectively. During each season, fragments and scrub matrix were surveyed during 3 consecutive days. Surveys in forest fragments followed the point-count methodology used by Willson et al. (1994). Point counts (stations) within each fragment had a fixed radius of 25 m and were at least 100 m apart to minimize the risk of counting the same individual twice, as suggested by Willson et al. (1994). Rhynocriptids were recorded only if observed within the fixed radius, because their loud calls can be heard more than 100 m away. We spent 8 minutes at each station. Because of differences in fragment area, survey effort was not equal. In small fragments (F1 and F2), only one point count was possible, and this was located at the center of the fragment to minimize the possibility of counting matrix species. In medium (F3 and F4) and large (F5 and F6) fragments, two and three point counts were used, respectively. This methodology did not allow us to obtain absolute abundances, so we calculated relative species abundance as the number of individuals per point per day. Each fragment also was surveyed daily in search of rare and inconspicuous species missed by the point-count surveys. To record the species present in matrix habitat, we carried out surveys of species along nine linear transects (M1–M9). Each transect was 100 m long and 30 m wide on each side. Stations within transects were distributed 20 m apart (Bibby et al. 1992). Transects M1 to M3 were located in the matrix scrub habitat around fragments in the mountain range. Transects M4 to M9 were located in the matrix scrub in the lowlands approximately 3 km away from the fragments. Transects were separated from one another by at least 1000 m. We also surveyed scrub habitat daily in search of rare and inconspicuous species. Nocturnal species (*Caprimulgus longirostris*) and raptors (*Bubo virginianus*, *Buteo polyosoma*, *Geranoaetus melanoleucus*, and *Falco* sp.) were not included in the analyses.

Data on the presence and absence of bird species were analyzed at local scales, comparing forest fragments to scrub sites in Fray Jorge, and at geographical scales, comparing the bird species assemblage at Fray Jorge's forest fragments and those inhabiting similar forests in southern Chile to those of nearby semiarid and mediterranean localities. The comparison was performed by unweighted pair-group method using arithmetic averages cluster analysis. Dissimilarity between sites was calculated according to the percent disagreement between sites. Data for sites other than Fray Jorge were obtained from Cody (1970; sites Cañete, Temuco, Puchuncaví, and Melipilla), Jaksic and Lazo (1999; site Aucó), Riveros and López-Calleja (1990; site Ocoa), López-Calleja (1990; site Quebrada de la Plata), Lazo and Anabalón (1992; site Tiltil), Willson et al. (1994; site Chiloé fragments), and Rozzi et al. (1996*a*; site Chiloé continuous forest). To assess the statistical significance of observed clusters, we performed a bootstrap analysis on the original presence-absence matrix, following the methodology described by Jaksic and Medel (1990).

To evaluate the effects of area on number of species, we used linear regression analysis between $\log_2$ number of species and $\log_2$ area (ha). To assess the effect of the strong isolation and relict character of our study system, we compared the species-area relationship calculated for the Fray Jorge forest fragments against that reported for temperate forest fragments located within Chiloé Island (Willson et al. 1994) and islands within the Chiloé Archipelago in southern Chile (Rozzi et al. 1996*a*).

Finally, to evaluate the existence of nonrandom patterns of species distribution across fragments, we tested for the existence of nestedness using the index C proposed by Wright and Reeves (1992). This index varies from 0 for a random pattern of distribution to 1 for a nested pattern and is independent of the number of sites and species analyzed, thus allowing for valid comparisons among systems. The statistical significance of *C* values was assessed with Cochran's *Q* test (Wright & Reeves 1992).

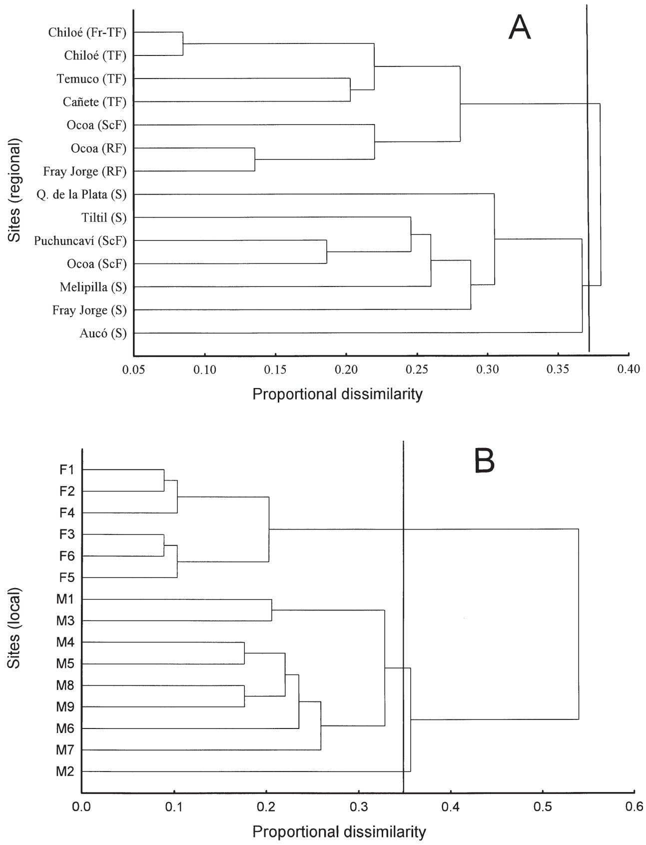

Figure 2. Cluster analysis using bird species composition (presence or absence) in different sites at (a) a regional scale and (b) a local scale in Fray Jorge National Park. Habitat types: (a) TF, temperate forest; RF, relict forest; Fr-TF, fragmented temperate forest; S, scrub; and ScF, sclerophyllous forests; and (b) scrub matrix habitat (M1-M9) and relict forest fragments (F1-F6). Vertical line indicates critical value of proportional dissimilarity.

Results

Geographic Analysis of Bird Species Assemblages

The cluster analysis at the regional scale showed two significant major clusters differing by 38% in their species composition (Fig. 2a). The bootstrapping analysis yielded a critical value for the linkage distance of 0.3729, so clusters that differed by more than this value were considered significantly different ($p \leq 0.05$). One cluster pooled forest bird assemblages, including Valdivian rainforest localities (e.g., Chiloé, Temuco) and Fray Jorge. The second cluster was composed of bird assemblages found in scrub and sclerophyllous forest habitats, including birds found in the scrub matrix habitat at Fray Jorge. The bird assemblage found in the relict forest of Fray Jorge is more similar in species composition to southern temperate forest localities and to the relict *Nothofagus* forest in Ocoa National Park than to those found in nearby scrub habitats. Similarly, at a local scale—forest fragments and scrub matrix sites within Fray Jorge—forest and scrub habitats were grouped into two distinct clusters (Fig. 2b). Forest fragments (F1–F6) shared <50 % of their species with scrub bird assemblages found in the matrix habitat (M1–M9) of Fray Jorge. Bootstrapping analysis yielded a critical value of 0.3529, so clusters that differed by more than this value were considered significantly different ($p \leq 0.05$). These results emphasize the similarity in species composition between the bird assemblage found in the relict Fray Jorge forest and those in temperate forests in southern Chile, and the dissimilarity between Fray Jorge and surrounding scrub areas.

Species Richness, Abundance, and Distribution in Relict Forest Fragments

We observed 37 bird species, in both forest fragments and matrix scrub habitat, belonging to the orders Passeriformes (28), Columbiformes (3), Apodiformes (2), Piciformes (2), Tinamiformes (1), and Galliformes (1) (Table 1). The latter was *Callipepla californica*, the only non-native species in the assemblage. We observed 21 species in forest fragments. Two species observed in autumn (*Sturnella loica* and *Diuca diuca*) and one observed in summer (*C. californica*) were observed only once during searches carried out at each fragment and therefore were not considered forest species (Table 1). Most of these forest species (85%) were year-round residents, and only two (*Aphrastura spinicauda* and *Colorhamphus parvirostris*) were endemic to southern South American temperate forests.

The most abundant species in forest fragments were *A. spinicauda* and *Sephanoides galeritus*. These species represented 45% of the total number of individuals counted, except in the spring survey when *S. galeritus* had a lower relative abundance, probably because part of the population migrated south and only a few individuals stayed to breed in large forest fragments. When present, *Elaenia albiceps* was also observed in high numbers. In general, *S. galeritus*, *Anairetes parulus*, *Troglodytes aedon*, *A. spinicauda*, *Turdus falcklandii*, and *Columba araucana* accounted for more than 65% of the total number of individuals observed in forest fragments. It should be noted that only the latter three species were restricted to forest habitat.

The number of bird species in each forest fragment was correlated positively with fragment area (Fig. 3). Although the number of species varied throughout the year, we found a significant relationship between fragment area and number of species in all seasons (autumn, $z = 0.204$, $r^2 = 0.909$, $p = 0.003$; winter, $z = 0.177$, $r^2 = 0.660$, $p = 0.049$; spring, $z = 0.215$, $r^2 = 0.910$, $p = 0.003$; summer, $z = 0.250$, $r^2 = 0.909$, $p = 0.003$). To test for the homogeneity of slopes and intercepts be-

Table 1. Bird species found in fragments (F) and scrub areas (M) of the Fray Jorge National Park forest (Chile).

Species[a]	*Common name*	*Family*	*Habitat*	*Residence*[b]
Nothoprocta perdicaria	Chilean Tinamou	Tinamidae	M	R
Callipepla californica	California Quail	Phasianidae	M	R
Columba araucana	Chilean Pigeon	Columbidae	F	R
Zenaida auriculata	Eared Dove	Columbidae	F-M	S
Columbina picui	Picui Ground-Dove	Columbidae	M	S
Patagona gigas	Giant Hummingbird	Trochilidae	F-M	S
Sephanoides galeritus	Green-backed Firecrown	Trochilidae	F-M	R
Picoides lignarius	Striped Woodpecker	Picidae	F-M	R
Colaptes pitius	Chilean Flicker	Picidae	F	R
Geositta cunicularia	Common Miner	Furnariidae	M	W
Upucerthia dumetaria	Scale-throated Earthcreeper	Furnariidae	M	W
Aphrastura spinicauda[a]	Thorn-tailed Rayadito	Furnariidae	F	R
Leptasthenura aegithaloides	Plain-mantled Tit-Spinetail	Furnariidae	F-M	R
Asthenes humicola	Dusky-tailed Canastero	Furnariidae	M	R
Pteroptochos megapodius	Moustached Turca	Rhinocryptidae	F-M	R
Scelorchilus albicollis	White-throated Tapaculo	Rhinocryptidae	F-M	R
Scytalopus magellanicus	Andean Tapaculo	Rhinocryptidae	F	R
Agriornis livida	Great Shrike-Tyrant	Tyrannidae	M	O
Muscisaxicola macloviana	Dark-faced Ground-Tyrant	Tyrannidae	M	W
Xolmis pyrope	Fire-eyed Diucon	Tyrannidae	F-M	R
Elaenia albiceps	White-crested Elaenia	Tyrannidae	F-M	S
Anairetes parulus	Tufted Tit-Tyrant	Tyrannidae	F-M	R
Colorhamphus parvirostris[a]	Patagonian Tyrant	Tyrannidae	F	W
Phytotoma rara	Rufous-tailed Plantcutter	Phytotomidae	M	R
Tachycineta meyeni	Chilean Swallow	Hirundinidae	F-M	R
Troglodytes aedon	House Wren	Troglodytidae	F-M	R
Turdus falcklandii	Austral Thrush	Muscicapidae	F	R
Mimus thenca	Chilean Mockingbird	Mimidae	M	R
Anthus correndera	Correndera Pipit	Motacillidae	M	O
Zonotrichia capensis	Rufous-collared Sparrow	Emberizidae	F-M	R
Sturnella loyca	Long-tailed Meadowlark	Emberizidae	M	R
Curaeus curaeus	Austral Blackbird	Emberizidae	M	R
Phrygilus gayi	Grey-hooded Sierra-Finch	Fringillidae	F-M	R
Phrygilus fruticeti	Mourning Sierra-Finch	Fringillidae	M	R
Phrydilus alaudinus	Band-tailed Sierra-Finch	Fringillidae	M	O
Diuca diuca	Common Diuca-Finch	Fringillidae	M	R
Carduelis barbata	Black-chinned Siskin	Fringillidae	F	R

[a] *Temperate-forest endemic species according to Rozzi et al. (1996*b).
[b] *R, Resident; S, summer migrant; W, winter migrant; O, occasional visitors.*

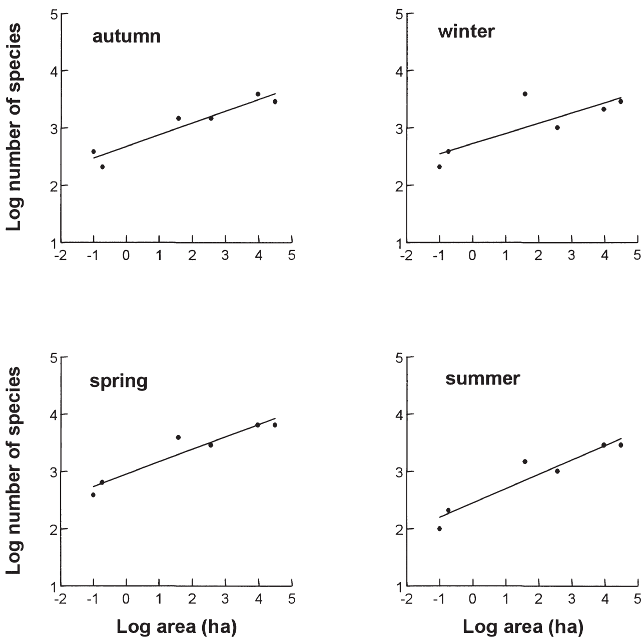

Figure 3. Seasonal variation in the species-area relationship for birds present in the relict forest fragments of Fray Jorge National Park.

tween seasons, we performed an analysis of covariance (ANCOVA), with area of the fragments as a covariate. Fragment area always had an effect on number of species ($F_{1,16} = 91.87, p = 0.0001$), but intercepts of regression lines were significantly different between seasons ($F_{3,16} = 3.91, p = 0.0285$), with a higher number of species (18) occurring during spring. No significant differences in the slopes of species-area curves for different seasons were found ($F_{3,16} = 0.47, p = 0.706$), however.

The distribution of species among forest fragments in Fray Jorge was not random. Although the nestedness varied seasonally, the system always had a significant (nonrandom) nested pattern of species distribution (Table 2), increasing in winter and spring when only forest-restricted species were considered (Table 2). We also found a significant and positive correlation between distribution (i.e., number of forest fragments in which a species was recorded) of bird species and their relative abundance in autumn ($r = 0.718, p = 0.008$), winter ($r = 0.698, p = 0.003$), spring ($r = 0.726, p = 0.004$), and summer ($r = 0.818, p = 0.001$), implying that low-abundance species tend to be narrowly distributed (Fig. 4). These latter species can be classified as rare. Throughout seasons, six species fit this category: *Colaptes pitius*, *C. parvirostris*, *Scytalopus magellanicus*, *Tachycineta meyeni*, *Carduelis barbata*, and *Picoides lignarius*. They were observed in three or fewer fragments at low relative abundance ranging from 1.3% to 6.3% of total individuals per fragment. *C. araucana* was found in no more than three fragments, but its relative abundance was higher (17%), probably due to its flocking behavior.

Table 2. Seasonal values of the nestedness index (*C*) and associated probability values (*p*), considering all species surveyed in the forest fragments (F-M and F in Table 1) and only species restricted to forest fragments (F in Table 1).

	All species		*Forest species*	
Season	*C*	p	*C*	p
Autumn	0.402	0.001	0.402	0.05
Winter	0.311	0.025	0.654	0.01
Spring	0.414	0.005	0.803	0.01
Summer	0.577	0.001	0.444	ns*

**Not significant.*

Relict Forest Bird Assemblage and Other Insular Habitats

The species-area curves for the Chiloé Archipelago and forest fragments within Chiloé Island were highly significant ($r^2 = 0.599, p = 0.002, n = 13$; and $r^2 = 0.899, p = 0.0001, n = 10$; respectively; Fig. 5). An ANCOVA revealed that area had a significant effect on the number of species found in fragments within Chiloé and across islands in the archipelago ($F_{1,18} = 47.13, p = 0.0001$), but they had different intercepts. For similar areas, forest fragments always had a higher number of species than did islands ($F_{1,19} = 14.74, p = 0.001$). We also found that the species-area relationship of both systems did not differ in slope ($F_{1,19} = 0.03, p = 0.87$). The slope value for the Chiloé Archipelago was 0.096; for fragments within Chiloé it was 0.101. The slope of the species-area relationship for forest fragments in Fray Jorge (Fig. 5) was significantly steeper than the slope calculated for the Chiloé Archipelago ($F_{4,27} = 2.93, p = 0.04$) and for fragments within Chiloé ($F_{4,24} = 4.57, p = 0.0069$).

Discussion

The bird assemblage found in Fray Jorge forest fragments is a subset of the assemblages found in South American temperate forests. They are not only similar in composition, as shown by cluster analysis, but are also similar with regard to the relative abundance of species. *S. galeritus*, *E. albiceps*, *A. spinicauda*, and *T. falcklandii* were among the most abundant species in southern temperate forests (Rozzi et al. 1996*b*) and were numerically dominant in the relict forest of Fray Jorge. The existing similarity between bird assemblages in the relict forest of Fray Jorge and the Valdivian temperate forest implies that these ecosystems are comparable, thus validating the use of the former to infer the potential long-term effects of fragmentation and isolation on the latter.

Fragment area is one of the major factors determining species loss in fragmented landscapes (Blake 1987; Blake

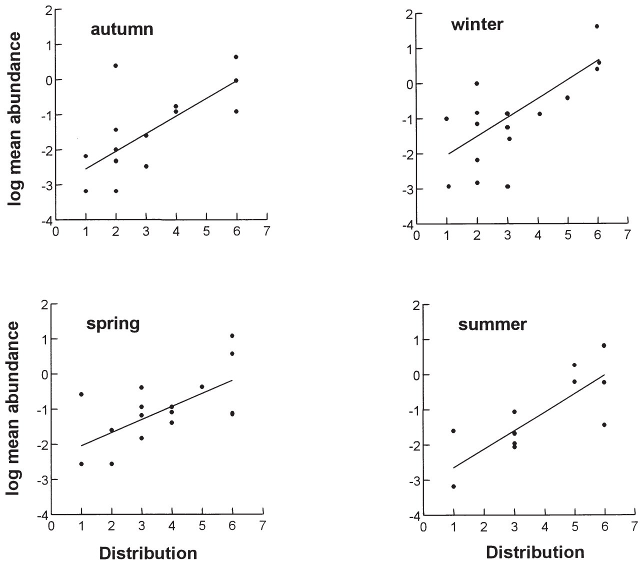

Figure 4. Seasonal variation in the relationship between bird species distribution (number of fragments occupied) and their mean abundance.

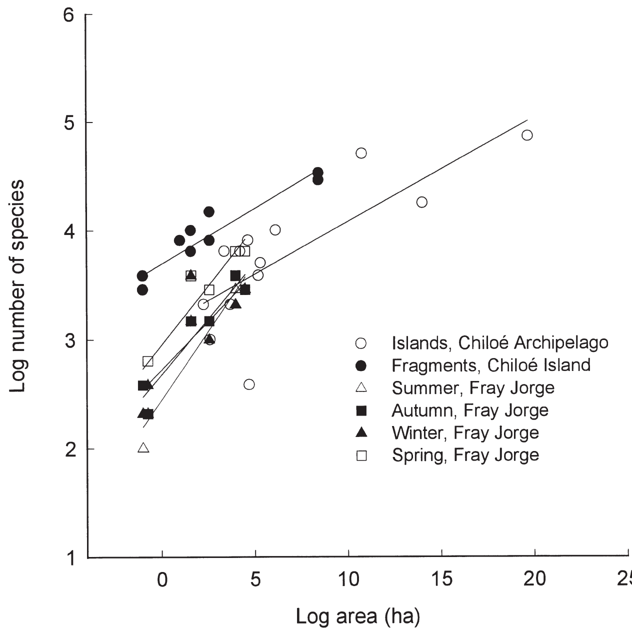

Figure 5. Species-area relationship for the relict forest fragments in Fray Jorge for southern temperate forests fragments within the island of Chiloé (from Willson et al. 1994) and across islands within the Chiloé Archipelago (from Rozzi et al. 1996a).

& Karr 1987; Soulé et al. 1992; Faaborg et al. 1995; Tellería & Santos 1997), and our study system is no exception to this rule. We found a strong positive relationship between the area of forest fragments and number of species. The slope of this relationship was not statistically different among seasons, with area explaining between 66% and 91% of the variation in species number. But we did find seasonal differences in the intercepts of regression lines (higher in spring), which may be accounted for by the arrival of spring and summer migrants (*Zenaida auriculata*, *Patagona gigas*, and *Elaenia albiceps*).

Our analysis of slope values revealed that, at the local scale and in any given season, independent of changes in the number of species, the rate of species loss with decreasing area remained the same. In Fray Jorge, z values ranged from 0.177 to 0.250. Lawlor (1986) reported similar values of z for volant mammals in oceanic archipelagoes. The equilibrium theory of island biogeography (MacArthur & Wilson 1967) predicts that the number of species on an island is the result of a balance between colonization and extinction rates, which are determined by area and isolation of the islands. For volant vertebrates (bats and birds) it is expected that such balance leads to higher z values in isolated oceanic islands than in landbridge islands located nearer the mainland (Lawlor 1986). In oceanic archipelagoes, steeper slope values result from greater isolation, which reduces the probability that species that become too rare can be rescued from extinction through immigration from nearby islands. This process is especially important on small islands.

The relict forest system had a steeper species-area slope than that reported for similar temperate-forest bird assemblages in forest fragments within Chiloé Island and for islands across the Chiloé Archipelago. Comparing the latter two systems, fragments in Chiloé (the largest island within the archipelago) contained a larger number of species than did islands of comparable size found in the archipelago, but their species-area slopes were not different. In this regard, the bird fauna in Fray Jorge resembles a depauperate oceanic archipelago. We considered this difference in area effects to be a consequence of the minimization of rescue effects because of the absence of large source forest areas and the long-term isolation of this system. These results strongly suggest that the Fray Jorge forest has already paid its extinction debt.

The bird species distribution among forest fragments in Fray Jorge was not random: we found a significantly nested distribution pattern. Our results indicate that nestedness was affected by the occurrence of some species common in the nearby matrix which occupied forest fragments secondarily (Table 1). When these species were left out of the analysis, nestedness increased for winter and spring seasons (Table 2); thus, the nestedness values observed were affected by "colonization noise" attributable to species not restricted to forest habitats. A nested pattern of distribution implies that some species are found across all sites, regardless of their area, and therefore are less affected by habitat fragmentation and less prone to local extinction (Atmar &

Patterson 1993; Wright et al. 1998). The existence of a positive correlation between abundance and distribution supports this claim.

Missing Species

For southern South American temperate forest, Rozzi et al. (1996*b*) described a bird assemblage of 31 nonraptor species corresponding to the orders Ciconiformes, Columbiformes, Psittaciformes, Apodiformes, Piciformes, and Passeriformes. Only 17 of these species were present in the relict forest in Fray Jorge.

Analyzing the distribution of the 14 southern temperate-forest species not found in the relict forest, we found that some had a wider distribution range than the temperate forest itself and/or occupy other habitats as well. This is the case for *Curaeus curaeus*, *Phytotoma rara*, *Pygochelidon cyanoleuca*, and *Theristicus melanopis* (the first two species were found in the lowland scrub at Fray Jorge). The absence of these species from the Fray Jorge forest may be a reflection of selection for scrub or other open-habitat types more than of their inability to persist in forest fragments. This explanation does not apply, however, to species endemic to the temperate forest, such as *Enicognathus ferrugineus* and *E. leptorhynchus* (Psittaciformes), *Campephilus magellanicus* (Piciformes), *Phrygilus patagonicus* (Fringillidae), *Pygarrhichas albogularis*, *Sylviorthorhynchus desmursii* (Furnariidae), *Eugralla paradoxa*, *Pteroptochos castaneus*, *P. tarnii*, and *Scelorchilus rubecula* (Rhinocryptidae). Among these species *C. magellanicus* is restricted mostly to mature beech (*Nothofagus*) forests (Fjeldså & Krabbe 1990), a forest type not represented at Fray Jorge. In addition, we recently (April 1999) found *P. albogularis* inhabiting a relict forest (Cerro Santa Inés) located on the coastal range 160 km to the south of Fray Jorge. This suggests that the absence of this species in Fray Jorge may be a consequence of the extreme isolation of this system. Most of the other species, however, have been found in forests similar to Fray Jorge in southern Chile (Erazo 1984), but they are absent from other relict forests found along the coastal range of central Chile (Riveros & López-Calleja 1990; S. Reid, C. C., and O. Barbosa, personal observations). This suggests that they were not able to persist in the progressively isolated forest remnants during climatic changes throughout the Quaternary.

We hypothesize that these species are highly sensitive to habitat fragmentation and that their absence is associated with some particular traits such as large body size, poor dispersal ability across nonforest habitat, and/or habitat specialization. Evidence from similar forests (Willson et al. 1994; Sieving et al. 1996) and from other forests around the world (Opdam et al. 1985; Kattan 1992; Kattan et al. 1994) suggests that species with these combinations of traits are usually prone to extinction.

Sieving et al. (1996) tested the tolerance of endemic species of the temperate-forest understory (*Eugralla paradoxa*, *Pteroptochos tarnii*, *Scelorchilus rubecula*, and *Scytalopus magellanicus*, all Rhinocryptidae, and *Sylviorthorhynchus desmursii*, Furnariidae) to flying across different matrix habitats (open pastures, scattered cover, and dense cover habitat) on Chiloé Island. They found that no species entered open pastures and that *S. magellanicus* is the species most prone to enter scattered-cover matrix habitat. Of the five understory forest species tested by Sieving et al. (1996), *S. magellanicus* was the only one found at Fray Jorge. This result lends partial support to the hypothesis that from the original stock of temperate forest species only those tolerant to isolation and area reduction were able to persist in Fray Jorge and other forest remnants in central Chile. Further studies to test this hypothesis are needed to rule out other potential causes linked to specific habitat or food requirements of some species.

Birds of Southern Temperate Forests

One of our main objectives was to take advantage of a natural experiment in habitat isolation to understand and foresee potential consequences of habitat fragmentation on southern temperate forests. Considering current rates of habitat loss, fragmentation, and degree of protection (Simonetti & Armesto 1991; Armesto et al. 1994, 1998; Bustamante & Grez 1995; Lara et al. 1996), this is a likely trajectory for southern Chilean forest landscapes. Our study showed that the effects of habitat fragmentation can be severe. In light of these results, we hypothesize that the most threatened species in southern temperate forests are those that could potentially be found but are presently absent at Fray Jorge. These are four endemic species in the family Rhinocryptidae (*Eugralla paradoxa*, *Pteroptochos castaneus*, *P. tarnii*, *Scelorchilus rubecula*); two endemic species in the family Furnariidae (*Sylviorthorhynchus desmursii*, *Pygarrhichas albogularis*); and the two endemic species in the family Psittacidae (*Enicognathus ferrugineus*, *E. leptorhynchus*). In addition to this group of species, our analysis of the Fray Jorge forest also identified another group that, by virtue of their low population densities and restricted distribution across habitat fragments, also should be considered of conservation concern: *Colaptes pitius*, *Carduelis barbata*, *Columba araucana*, *Colorhamphus parvirostris*, and *Scytalopus magellanicus*. The latter two species also were recognized by Willson et al. (1994) as sensitive to habitat fragmentation.

Conservation and Management Implications

In our system, fragment area had a strong effect on number of species. This result by itself, however, is not informative enough to support recommendations for the design of natural reserves or decisions among alternative management options. An additional piece of information is needed on the distribution of species on fragments of different area. Distribution data can help managers to decide whether a single large fragment (or reserve) or several small ones will protect more species in the temperate forest ecoregion (the persistent question of SLOSS). At one extreme, in systems where species show random occurrences across fragments of different areas, a collection of small fragments can potentially contain more species than a single large fragment of equivalent area (e.g., Quinn & Harrison 1988). At the other extreme, in systems with a perfectly nested pattern in species composition, a collection of small fragments (or reserves) will contain fewer species than a single large fragment (Brown 1986; Patterson 1987; Blake 1991; Atmar & Patterson 1993). The observed nestedness pattern and the positive correlation between number of species and fragment area found in Fray Jorge indicate the existence of a pronounced gradient in extinction vulnerability, suggesting that for temperate forest birds, large fragments (or reserves) should offer better protection against extinction than small, isolated forest patches.

But how large should this fragment be? Using the species-area relationship for Fray Jorge, an isolated system that already paid its extinction debt, we estimated that the minimum fragment area required to support the full complement of species expected in a similar but continuous temperate forest in southern Chile (38 species according to Rozzi et al. [1996*b*], excluding aquatic and raptor species) should be between 1639 and 19541 ha, with an average of 7428 ha. The first figure was obtained by using the species-area relationship calculated for the spring season, and the second by using the relationship obtained during winter. The average was calculated over all seasonal estimates calculated for Fray Jorge. These figures should be considered with caution. There is nothing better than hard data. To preserve temperate forest species, we need detailed studies of their demographic attributes and population viability as related to habitat quantity and quality.

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