

Differential effects of habitat fragmentation on birds and mammals in Valdivian temperate rainforests

Efectos diferenciales de la fragmentación del hábitat sobre aves y mamíferos del bosque valdiviano

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ABSTRACT

Four recent studies on Chilean vertebrates underscore the very different effects that habitat fragmentation may have under different conditions. In southern Chile, birds exhibited significant species-area relationships, whereas the more depauperate small mammal community did not. The avifauna of highly isolated rainforest remnants in Fray Jorge National Park (IV Región) presented steeper species-area relations than those in southern Chile, reminiscent of land-bridge islands after faunal relaxation. The small mammal results were unexpected but may reflect the reduced vagility and immigration potential of this group. Additionally, the inter-remnant matrix habitat may support large populations of only some species, allowing them to capitalize on resources that are available in forest remnants. Such an effect is less likely for birds due to their greater vagility. Although the influence of remnant area is more clearly demonstrated for birds in Chile, it appears that small mammal assemblages may be more immediately impacted by habitat fragmentation than are birds, and that further fragmentation of temperate rainforests will seriously impoverish the small mammal assemblage, many of whose members are endemic to this region. Further research should emphasize the role of the inter-remnant matrix, of habitat corridors, and of the relative sensitivity of different species to matrix/corridor quality and remnant isolation.

Key words: habitat fragmentation, Valdivian temperate rainforest, small mammals, birds, conservation.

RESUMEN

Cuatro estudios recientes en vertebrados chilenos subrayan los efectos muy diversos que la fragmentación del hábitat puede tener bajo diversas condiciones. En el sur de Chile, las aves exhibieron relaciones significativas entre la riqueza de especies y el área de hábitat ("especies-área"), mientras que tal relación no se observó en la comunidad de pequeños mamíferos, la cual tiene menos especies. La avifauna de los fragmentos remanentes altamente aislados del Parque Nacional Fray Jorge (IV Región) presentaron relaciones especies-área más pronunciadas que aquellas de Chile meridional. Lo observado para los pequeños mamíferos fue inesperado aunque puede reflejar un menor potencial de movilidad e inmigración en este grupo. Además, el hábitat de la matriz inter-fragmento puede albergar solo a poblaciones grandes de algunas especies, lo que les permitiría capitalizar los recursos que están disponibles en los fragmentos de bosque. Tal efecto es menos probable para el caso de las aves producto de su mayor movilidad. Aunque la influencia del área de los fragmentos remanentes es más claro en el caso de las aves en Chile, es probable que los ensambles de mamíferos pequeños sean más afectados en el corto plazo por la fragmentación del hábitat que las aves, y que una fragmentación adicional de los bosques templados lluviosos determinará un mayor empobrecimiento de los ensambles de pequeños mamíferos, muchos de los cuales son endémicos en esta región. Estudios adicionales deberían enfatizar el papel de la matriz inter-fragmento, el de los corredores de hábitat, y evaluar la sensibilidad relativa de diversas especies al aislamiento de los fragmentos remanentes y a la calidad de la matriz/corredor.

Palabras clave: fragmentación del ambiente, bosque lluvioso valdiviano, pequeños mamíferos, aves, conservación.

INTRODUCTION

The biota of the temperate rainforests of southern South America is diverse and of great biogeographic interest. The herpetofauna alone includes 20 species of anurans, six lizards, and two snakes (Formas 1979, these numbers are dated and likely underestimate the true diversity). The

avifauna is moderately diverse (Vuilleumier 1985 reports 46 species in 40 genera) but highly endemic (66 % of species [Rozzi et al. 1995], 10 % of genera [Vuilleumier 1985]). And while the mammal fauna is not highly diverse (Meserve & Jaksic 1991), it is similarly unique (six of nine genera are endemic, Patterson 1992). Overall, this area is notable for levels of endemism that

rival some of the world's hotspots such as Madagascar.

This region, the *Nothofagus* center of endemism (Cracraft 1985), has been given high priority for conservation by the International Council on Bird Preservation (International Council for Bird Conservation 1992), and overall is considered "endangered" and of outstanding regional value (Biodiversity Support Program 1995). The World Wildlife Fund has included the Valdivian temperate rainforest in its "Focal 25" areas for immediate conservation action and impact (see <http://www.worldwildlife.org/global200/spaces.cfm>). Unfortunately, protected areas in temperate Chile generally are at high elevation and higher latitudes, leaving most species in this region susceptible to ecologically unfriendly land management (Armesto et al. 1998, Defensores del Bosque Chileno 1998). The future of this region, therefore, hangs on the balance of political decisions that are being made often without sufficient biological background (e.g., Fuentes 1994, Lara et al. 1995). The future of the animals of these forests is directly dependent on the future of the forests themselves, and enlightened management decisions to guide the future of these global treasures rely on an understanding of the consequences of pending management decisions.

Four recent research programs have provided steps towards understanding the consequences of forest fragmentation in this system, but all suffer from taxonomically restricted focus. Willson et al. (1994), Gantz & Rau (1999), and Cornelius et al. (2000) studied avian communities, and Kelt (2000) studied small mammal communities, in fragmented forest habitats in Chile. Three of these studies (Willson et al. 1994, Gantz & Rau 1999 and Kelt 2000) were conducted in anthropogenic

forest fragments within areas recently covered by Valdivian rainforest, whereas the fourth study (Cornelius et al. 2000) was conducted in forest remnants that have been isolated from other temperate rainforests since the Quaternary. Perhaps surprisingly, the relationship between area and local species richness differed greatly between these three studies. The purpose of this commentary is to compare these four studies and to suggest avenues of future research.

Summary of these studies

Willson et al. (1994) studied the avifauna of 11 forest remnants on Isla Chiloé during the austral spring of 1992. Sites ranged in area from less than 0.5 ha to over 100 ha, but were not evenly distributed by size class. Unable to find any intermediate size fragments (e.g., 10-100 ha in area), their sample included three large patches (> 100 ha), five small remnants (0.1-10 ha), and three tiny remnants (< 0.5 ha). They also studied one secondary forest greater than 100 ha in area. They reported 25 regularly occurring bird species, most of which (60 %) were endemic to southern temperate forests. Species diversity declined markedly with remnant size (Table 1, Fig. 1), and with the exception of three edge species, virtually all species had lower abundances in smaller remnants.

Gantz & Rau (1999) evaluated avian diversity in 18 forest remnants in the province of Osorno in 1996 and 1997. Remnants here ranged from 3 to 344 ha with a fairly even distribution of sizes. Species richness ranged from eight to 19 species, and a total of 32 species were recorded. These authors also demonstrated a clear relationship

TABLE 1

Regression statistics for birds in temperate rainforest remnants in southern and north-central Chile, and for mammals in rainforest remnants in southern Chile. Sources: (1) Willson et al. (1994), (2) Gantz & Rau (1999), (3-6) Cornelius et al. (1999), (7) Kelt (2000)

Estadísticas de regresión para aves en fragmentos de bosque remanentes del sur y centro-norte, y para mamíferos pequeños en fragmentos de bosque remanentes del sur de Chile. Fuentes: (1) Willson et al. (1994), (2) Gantz & Rau (1999), (3-6) Cornelius et al. (1999), (7) Kelt (2000)

Study	n	Intercept	Slope	F-value	P-value	r ² -value
(1) Birds, Chiloé	10	3.69 (0.049)	0.101 (0.012)	71.24	0.0001	0.8990
(2) Birds, Osorno	18	3.03 (0.216)	0.148 (0.038)	14.78	0.0014	0.4801
(3) Birds, Fray Jorge, May	6	2.68 (0.090)	0.204 (0.032)	40.08	0.0032	0.9093
(4) Birds, Fray Jorge, August	6	2.72 (0.177)	0.177 (0.064)	7.77	0.0494	0.6603
(5) Birds, Fray Jorge, December	6	2.95 (0.094)	0.215 (0.034)	40.48	0.0031	0.9101
(6) Birds, Fray Jorge, March	6	2.44 (0.111)	0.250 (0.040)	39.80	0.0032	0.9087
(7) Mammals, southern Chile	18	2.00 (0.187)	-0.006 (0.055)	0.012	0.9142	0.0007

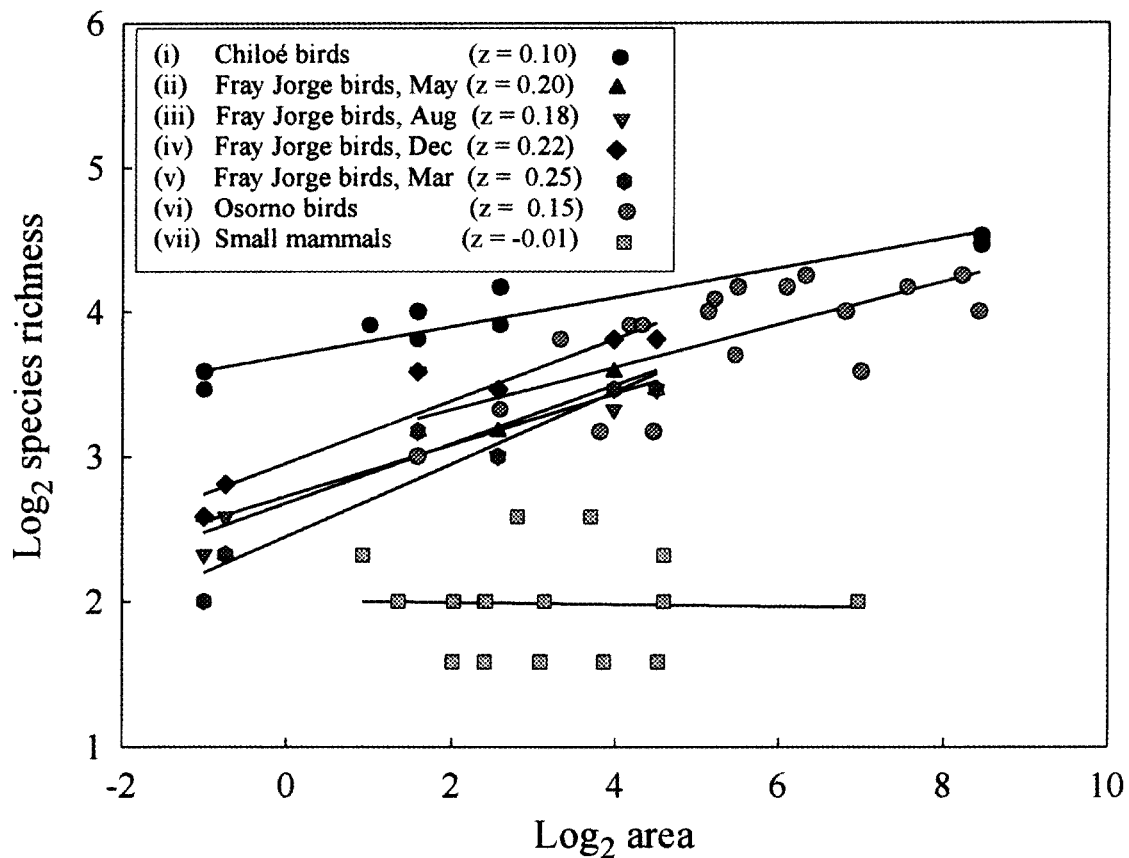


Fig. 1: Species-area relationships for four recent studies conducted in Chile. Willson et al. (1994) and Gantz & Rau (1999) studied birds, and Kelt (2000) studied mammals, both in remnants of Valdivian temperate rainforest, whereas Cornelius et al. (2000) studied the avifauna of forest patches in north-central Chile. Presented are summary data and species-area relationships. The slope of these relationships (z-values) is given in the legend.

Relaciones especie-área para cuatro estudios recientes realizados en Chile. Willson et al. (1994) y Gantz & Rau (1999) estudiaron aves y Kelt (2000) mamíferos pequeños en fragmentos de bosque valdiviano, mientras que Cornelius et al. (2000) analizaron la avifauna en parches de bosque de Chile centro-norte. Se incluye un resumen de los datos y de las relaciones especie-área. La leyenda incluye las pendientes (valores de z) de estas relaciones.

between remnant area and species richness (Table 1, Fig. 1).

Cornelius et al. (2000) censused the avifauna of six forest fragments located in north-central Chile. Over the course of a year these patches, ranging from 0.5 to 22.5 ha in area, were sampled with methods similar to those employed by Willson et al. (1994). Unlike the forest remnants studied in southern Chile, the forests studied by Cornelius et al. (2000) were protected from human intervention by their presence within Parque Nacional Fray Jorge. Also unlike other studies summarized here, the forests at Fray Jorge have been isolated from continuous temperate rainforest since the Quaternary, but have persisted at this locality because the coastal hills trap extensive fog (the "camanchaca") and provide a substantial

supplement to the mean annual rainfall of 85 mm. Because of this extensive period of isolation the forests at Fray Jorge provide insights into the long-term impacts of forest fragmentation, and may bear important insights for managers of the forests found in southern Chile and Argentina. Cornelius et al. (2000) encountered 21 species of birds in their forest samples (another 16 species were recorded in adjacent matorral habitats but did not venture into the forests), and they found species richness to be strongly and positively correlated with remnant area in all seasons studied (Table 1). Moreover, the species-area relationship was similar in all four seasons studied (ANCOVA, Table 2A).

Only one study has been conducted on the distribution of mammals in temperate rainforest

TABLE 2

Analysis of covariance results comparing the regression slope (species-area relation, z-values) across seasons for birds at (A) Fray Jorge and (B) across all three studies with all data pooled within studies

Resultados del análisis de covarianza utilizado para comparar las pendientes (de relaciones especie-área, valores de z) entre estaciones en (A) Fray Jorge y (B) entre los tres estudios con los datos agrupados dentro de cada estudio

(A) Fray Jorge birds

Source	Degrees of freedom	Mean square	F-value	P-value
Model	7	0.7858	15.02	0.0001
Season	3	0.1478	2.83	0.0719
Slope	1	4.8120	91.97	0.0001
Season x slope	3	0.0247	0.47	0.7057
Error	16	0.0523		

(B) All four studies

Source	Degrees of freedom	Mean square	F-value	P-value
Model	7	6.5256	83.71	0.0001
Study	3	2.4368	31.26	0.0001
Slopes	1	3.2872	42.17	0.0001
Study*Slopes	3	0.4913	6.30	0.0008
Error	62	0.0780		
Contrast				
Cornelius vs. Kelt	1	4.4482	60.14	0.0001
Cornelius vs. Willson	1	6.0820	82.23	0.0001
Willson vs. Kelt	1	1.2386	16.75	0.0002
Gantz vs. Willson	1	0.6568	8.43	0.0051
Gantz vs. Cornelius	1	0.1777	2.28	0.1362
Gantz vs. Kelt	1	1.2377	15.88	0.0002

remnants. Kelt (2000) sampled the small mammal assemblages in 14 remnants in the same area as Gantz & Rau (1999). Located in a similar system to that studied by Willson et al. (1994), both Kelt (2000) and Gantz & Rau (1999) studied forest remnants within a largely agricultural mosaic. Kelt (2000) reported on remnants ranging from ca. 0.5 to 125 ha in size, all of which were sampled with extensive trapping during two winter seasons (1985 and 1986), when populations generally are greatest in this system (Meserve et al. 1991). Additionally, four remnants were sampled in both years of study (for a total of 18 samples). In contrast to the relatively speciose avifaunas of these habitats, the total small mammal fauna included only six native rodents and two marsupials. In marked contrast to both avian studies, and in spite of a larger number of remnants sampled than in two of the avian studies, Kelt found no indication of any area effects, either on species richness (Table 1), estimated population

size (captures per unit effort), or species diversity (H' , Kelt 2000). Extensive vegetative metrics also failed to suggest any habitat features associated with measures of biotic structure (Kelt 2000).

Although six of the bird species recorded at Fray Jorge were not recorded by Willson et al. (1994), and the latter recorded nine species not reported by Cornelius et al. (2000), the Fray Jorge avifauna was a subset of the Valdivian avifauna, both in terms of species composition and relative abundances (Cornelius et al. 2000). Gantz & Rau (1999) did not provide a list of the species in their study, but it was undoubtedly typical of the Valdivian avifauna as well. Consequently it seems reasonable to compare these studies in terms of general responses to habitat fragmentation. The broad overlap in the study areas of Kelt (2000) and Gantz & Rau (1999) also support cross-taxon comparisons between these studies.

Comparison of responses to fragmentation

The species-area relations across these studies differ significantly (ANCOVA), and a priori contrasts demonstrated that most studies differ significantly from each other (Table 2B). The z -value calculated for the avifauna studied by Gantz & Rau (1999) does not differ from that observed at Fray Jorge (Table 2B), although it is significantly steeper than that observed by Willson et al. (1994) on Isla de Chiloé. Although these contrasts should be evaluated cautiously, as it is not technically valid to perform all of these contrasts, it is apparent that dramatic differences exist among these studies.

In comparing their results with those from Chiloé, Cornelius et al. (2000) noted that the forest habitat at Fray Jorge has been restricted to its present distribution since the Quaternary. The nearest extensive Valdivian rainforests presently are >1,200 km south of Fray Jorge, leading Cornelius et al. (2000) to predict that the Fray Jorge fauna would be depauperate, that it would yield a species-area relationship more similar to true (oceanic) islands than to land-bridge islands, and that this system had "already paid its extinction debt" (pp. 535). Implicit in the prediction of an oceanic z -value is that most bird species present in these remnants have arrived since isolation, rather than representing a relictual post-isolation fauna (Lawlor 1986). In fact, three of the four seasonal z -values obtained by these authors were > 0.20, more similar to the mammal faunas of land-bridge islands than to the oceanic islands summarized by Lawlor (1986), but intermediate between the "island curves" ($z \approx 0.25$ -0.33) and the "mainland curves" ($z \approx 0.13$ -0.18) outlined by Rosenzweig (1995), and substantially lower than the $z = 0.34$ exhibited by birds in 23 Páramo "islands" (Viulleumier & Simberloff 1980). And while the assemblages at Fray Jorge ($S = 21$ species) had fewer species than those in southern Chile ($S = 25$ and 32), it is not clear if this is "depauperate" relative to the presumed source fauna ($S = 46$, Viulleumier 1985). Certainly the remnants at Fray Jorge include some species that are not members of the Valdivian rainforests avifauna (e.g., *Patagona gigas* (Vieillot), *Asthenes humicola* (Kittlitz), but most species encountered are represented in the southern avifauna (Cornelius et al. 2000). At any rate, the remnants at Fray Jorge do not seem inordinately depauperate relative to remnant forests near Osorno (Gantz & Rau 1999) or on Isla de Chiloé (Willson et al. 1994).

Because true oceanic islands experience low rates of immigration, regardless of size, Lawlor

(1986) noted that they should have low species richness as well as low species-area relations. Land-bridge islands, in contrast, should be driven by differential extinction on large vs. small islands, with smaller islands losing more species. Consequently, these should have steeper z -values and range from low to high richness on small and large remnants, respectively. Thus, higher z -values are to be expected either when post-isolation extinction has been greater in small than large remnants, or when immigration is sufficiently high that large remnants can accumulate species that cannot survive on smaller remnants (a third possibility, operating over evolutionary time scales, invokes greater in situ speciation on larger islands, but this is not relevant to the habitat remnants under consideration here). Of particular interest is that the former explanation invokes differential extinction on large vs. small remnants, whereas the latter invokes differential immigration. Data from Fray Jorge are somewhat inconclusive, as z -values fall in a rather vague area between that expected for oceanic islands and that for land-bridge islands (see above), but it seems likely that the extant avifauna has indeed relaxed from an initially higher species richness. Further work aimed at teasing apart these two explanations, perhaps involving genetic comparisons of Fray Jorge populations with those in contiguous Valdivian forests of southern Chile, would be particularly interesting. In contrast to the avifauna of Fray Jorge, bird faunas in fragmented habitats of southern Chile (Willson et al. 1996, Gantz & Rau 1999) yielded lower slopes but high species richness that generally are more typical of continental habitat fragments (Lawlor 1986).

The lack of a significant species-area relationship for small mammals was initially surprising, as such relationships have been reported elsewhere (e.g., Dunstan & Fox 1996, Rosenblatt et al. 1999, Nupp & Swihart 2000). Mammal faunas typically are depauperate relative to avifaunas, however, and it is possible that the limited mammal fauna of the Valdivian forests precluded a significant relationship. It seems more likely, however, that mixed management of "matrix" habitat allowed for extensive dispersal by common species (especially *Abrothrix olivaceus* (Waterhouse, 1837), *A. longipilis* (Waterhouse, 1837), and *Oligoryzomys longicaudatus* (Bennett, 1832), which occurred in all remnants and comprised over 98 % of captures) but only moderate dispersal by most other species (see Malcolm 1997, Kelt 2000). In the structurally similar rainforests of the Olympic Peninsula of Washington, Lomolino & Perault

(2001) studied a mammal fauna with 18 species, also reporting a non-significant species-area relationship. Although the largest remnant reported by Lomolino & Perault (2001) was less than 60 ha in area, Kelt (2000) surveyed one remnant in excess of 120 ha. Both papers suggested that the lack of a significant relationship exemplified the "small island effect," which occurs when no sites are sufficiently large to generate a positive slope (Brown & Lomolino 1998). Both studies also echoed earlier suggestions (Malcolm 1997) that matrix habitat may support habitat generalists, thereby increasing the representation of these species in isolated habitats, as well as the impact of these species on any individuals of more specialist species.

Superficially these results might suggest that the avifauna of southern temperate rainforests are more likely to be adversely impacted by continued habitat fragmentation than is the mammal fauna. This is not necessarily true, however, as the distribution of small mammals reported by Kelt (2000) was really quite heterogeneous. Reliance upon the species-area relationship may obfuscate a number of details that may be important, and it also ignores the broader ecological context in which habitat remnants exist. Although most bird species declined in habitat remnants on Chiloe, three edge species (*Turdus falcklandii* Quoy and Gaimard, *Troglodytes aedon* Vieillot, and *Zonotrichia capensis* (Müller)) increased significantly. Similarly, three of the seven native species encountered by Kelt (2000) (excluding *Loxodontomys micropus* (Waterhouse, 1837) which was only captured in intervening habitats) were present in all remnants, and constituted the vast majority of captures. The remaining species included the endemic *Irenomys tarsalis* (Philippi, 1900) (12 captures in seven remnants), *Geoxus valdivianus* (Philippi, 1858) (nine captures in seven remnants), *Dromiciops gliroides* Thomas, 1894 (three captures in two remnants), and *Rhyncholestes raphanurus* Osgood, 1924 (one capture). Moreover, four mammal species found in this region had lower abundances in remnants than in nearby contiguous habitat (Kelt 2000). Clearly, reliance only upon the simplistic species-area relationship fails to account for factors that influence the abundance and distribution of these taxa (e.g., Harrison & Bruna 1999). Importantly, these observations suggest that ongoing fragmentation is highly likely to have a negative impact on the mammalian assemblage of this region, and possibly more so than for birds, and the ecology of these species should be considered in ongoing management decisions.

The future

In their assessment of the conservation status of terrestrial mammals in Chile, Cofré & Marquet (1999) noted that the Matorral region contains a larger number of endemic species than any major biotype in Chile, is particularly threatened by habitat loss and degradation, and is poorly protected by the national system of parks and reserves. Although the temperate rainforests of southern Chile did not emerge as highly threatened in their analysis, this likely was a consequence of the fact that the southern region has fewer species than the matorral region of Chile, and therefore did not yield large summary statistics. Mediterranean regions are threatened globally (e.g., Rundel et al. 1988, Mittermeier et al. 1998, Olsen & Dinerstein 1998), and it might be argued that future efforts to protect additional parts of these biomes from human encroachment are tightly constrained. Fortunately, the case for temperate rainforests is not quite as severe; although these ecosystems also are poorly represented in Chile's system of protected areas (Armesto et al. 1998) and they are heavily impacted by extractive industries (Ecotrust/Conservation International 1992, Donoso & Lara 1995), it may yet be possible to plan for their biotic maintenance. With respect to the Valdivian forests of southern Chile and Argentina, it is clear that further work is needed in many facets of the ecology of various species. We presently have no information on the responses of most temperate groups to habitat fragmentation or degradation. Several points and recommendations emerge from this commentary.

First, the importance of the habitat matrix in which forest remnants are isolated appears to be critical to the post-isolation dynamics of the remnants. The importance of matrix habitat has been emphasized both in tropical (e.g., Lynam 1997, Malcolm 1997) and temperate (e.g., Kelt 2000, Lomolino & Perault 2001) systems, and may greatly influence the character of remnant faunas, both in terms of the species present and their relative numbers. Further research on how matrix characteristics influence both the composition and the demography of remnant faunas should be given high priority.

Second, for most taxa we remain woefully ignorant of the role of habitat edge on the activity patterns of various species. While many predators are most active along habitat edges and may greatly influence the composition of the remnant fauna (e.g., Heske 1995, Robinson et al. 1995), some non-predatory taxa also prefer edge habitats (e.g., Willson et al. 1996, Lomolino & Perault 2001), which may provide an agreeable combination of

cover and food. Of course, edge is perceived very differently by different taxa (e.g., butterflies vs. birds vs. small mammals in Amazonia; see papers in Laurance & Bierregaard 1997), so it may be difficult, if not impossible, to generalize any specific effects across taxa.

Third, synergistic effects of remnant area, isolation, and habitat on the faunal composition of habitat remnants have been documented in Australia (e.g., Dunstan & Fox 1996) and North America (Lomolino & Perault 2001). Further work in Chilean and Argentine forests should employ a broader geographic scale than the studies summarized here, employing GIS and remote imaging to better quantify remnant features as well as details of matrix habitat. The basic island biogeography paradigm is no longer suitable for understanding the complexities of fragmented, often multiply interconnected habitats (Harrison & Bruna 1999).

Fourth, patterns of individual movement need to be investigated to understand how species use fragments of differing sizes and shapes. Different species may exhibit unexpected patterns of movement among and within habitat remnants (e.g., Diffendorfer et al. 1995), rendering predictions based on research in primary forest unreliable at best.

Fifth, differential sensitivity to secondary habitat degradation is likely to influence some species more than others. Habitat changes often associated with fragmentation in South America include invasion by cattle and removal of wood for fuel. Arboreal species (e.g., many birds, the Chilean tree mouse *Irenomys*, the monito del monte *Dromiciops*) and species that forage in the litter (e.g., *Geoxus*, *Rhyncholestes*, birds in the family Rhynchocryptidae) may be more heavily impacted by such activities than by the size or isolation of the remnant or by characteristics of the habitat matrix. It is likely that some form of management will be needed to allow partial exploitation of forest remnants while maintaining critical structural and biotic features that allow the survival of these species.

Finally, and perhaps most important in the face of certain continued forest exploitation, is the question of how habitat remnants and corridors should be designed to maximize the probability of inter-remnant movement. While research has begun to quantify habitat barriers (Sieving et al. 1996) and corridor needs by Valdivian forest birds (Sieving et al. 2000), no information is available on the requisite structure or size of corridors for mammalian habitat specialists such as *Irenomys tarsalis*, *Dromiciops gliroides*, *Geoxus valdivianus*, and *Rhyncholestes*

raphanurus, nor for larger mammals such as the the guiña (*Oncifelis guina*) or the endemic pudu (*Pudu puda*). These species are likely to be threatened by extensive habitat alteration, and should be the focus of research while time remains to develop sound management plans.

The temperate forests of Chile and Argentina constitute an ideal system to compare against the extensive results from fragmented environments in North America, Europe, and Australia (e.g., Burgess & Sharpe 1981, Harris 1984, Wilcove et al. 1986, Robinson et al. 1995, and papers in Lidicker 1995, Dunston & Fox 1996, McCullough 1996, Barrett & Peles 1999, Lomolino & Perault 2000, 2001, Perault & Lomolino 2000), and to validate or modify conclusions drawn there. Substantial progress has been made towards such objectives (e.g., Donoso 1993, Armesto et al. 1995), but much remains to be done. Further efforts towards the questions outlined here will greatly increase the ability of landscape and economic managers alike to plan for rational, and hopefully sustainable, utilization of the Valdivian (and Fuegian) temperate rainforests. None of these are logistically difficult problems, and all may be addressed relatively easily. Without a concerted effort, however, it is virtually certain that the biodiversity of temperate South America will become impoverished in the face of the global economy.

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LITERATURE CITED

- ARMESTO JJ, R ROZZI, C SMITH-RAMÍREZ & MTK ARROYO (1998) Conservation targets in South American temperate forests. *Science* 282: 1271-1272.
- ARMESTO JJ, C VILLAGRÁN & MK ARROYO (eds) (1995) *Ecología de los bosques nativos de Chile*. Editorial Universitaria, Santiago, Chile. 477 pp.
- BARRETT GW & JD PELES (eds) (1999) *Landscape ecology of small mammals*. Springer-Verlag, New York, New York. xix + 347 pp.

- BIODIVERSITY SUPPORT GROUP (1995) A regional analysis of geographic priorities for biodiversity conservation in Latin America and the Caribbean. Corporate Press, Landover, Maryland. xxiii + 116 pp.
- BROWN JH & MV LOMOLINO (1998) Biogeography. Second edition. Sinauer Associates, Sunderland, Massachusetts. xii + 691 pp.
- BURGESS RL & DM SHARPE (eds) (1981) Forest island dynamics in man-dominated landscapes. Springer-Verlag, New York, New York. xvii + 310 pp.
- COFRÉ H & PA MARQUET (1999) Conservation status, rarity, and geographic priorities for conservation of Chilean mammals: an assessment. *Biological Conservation* 88: 53-68.
- CORNELIUS C, H COFRÉ & PA MARQUET (2000) Effects of habitat fragmentation on bird species in a relict temperate forest in semiarid Chile. *Conservation Biology* 14: 534-543.
- CRACRAFT J (1985) Historical biogeography and patterns of differentiation within the South American avifauna: areas of endemism. *Neotropical Ornithology* 36: 49-84.
- DEFENSORES DEL BOSQUE CHILENO (1998) La tragedia del bosque Chileno. Ocho Libros Editores Ltda., Santiago, Chile. 395 pp.
- DIFFENDORFER JE, MS GAINES & RD HOLT (1995) Habitat fragmentation and movements of three small mammals (*Sigmodon*, *Microtus*, and *Peromyscus*). *Ecology* 76: 827-839.
- DONOSO ZC (1993) Bosques templados de Chile y Argentina. Editorial Universitaria, Santiago, Chile. 484 pp.
- DONOSO C & A LARA (1995) Utilización de los bosques nativos en Chile: pasado, presente y futuro. In: Armesto JJ, C Villagrán & MK Arroyo (eds) *Ecología de los bosques nativos de Chile*: 363-387. Editorial Universitaria, Santiago, Chile.
- DUNSTON CE & BJ FOX (1996) The effects of fragmentation and disturbance of rain forests on ground-dwelling small mammals on the Robertson Plateau, New South Wales, Australia. *Journal of Biogeography* 23: 187-201.
- ECOTRUST/CONSERVATION INTERNATIONAL (1992) Coastal temperate rain forests: ecological characteristics, status and distribution worldwide. Occasional Paper Series 1: 1-64.
- FORMAS JR (1979) La herpetofauna de los bosques templados de Sudamérica. In: Duellman WE (ed) *The South American herpetofauna: its origin, evolution, and dispersal*: 341-369. Museum of Natural History, University of Kansas, Monograph 7.
- FUENTES E (1994) ¿Qué futuro tienen nuestros bosques?: hacia la gestión sustentable del paisaje del centro y sur de Chile. Ediciones Universidad Católica, Santiago, Chile. 290 pp.
- GANTZ A & J RAU (1999) Relación entre el tamaño mínimo de fragmentos boscosos y su riqueza de especies de aves en el sur de Chile. *Anales del Museo de Historia Natural de Valparaíso (Chile)* 24: 85-90.
- HARRIS LD (1984) The fragmented forest: island biogeographic theory and the preservation of biotic diversity. University of Chicago Press, Chicago, Illinois. xviii + 211 pp.
- HARRISON S & E BRUNA (1999) Habitat fragmentation and large-scale conservation: what do we know for sure? *Ecography* 22: 225-232.
- HESKE EJ (1995) Mammalian abundances on forest-farm edges versus forest interiors in southern Illinois: is there an edge effect? *Journal of Mammalogy* 76: 562-568.
- INTERNATIONAL COUNCIL FOR BIRD PRESERVATION (1992) Putting biodiversity on the map: priority areas for global conservation. International Council for Bird Preservation, Cambridge, United Kingdom. vi + 90 pp.
- KELT DA (2000) Small mammal communities in rainforest fragments in central southern Chile. *Biological Conservation* 92: 345-358.
- LARA A, C DONOSO & JC ARAVENA (1995) La conservación del bosque nativo de Chile: problemas y desafíos. In: Armesto JJ, C Villagrán & MK Arroyo (eds) *Ecología de los bosques nativos de Chile*: 335-362. Editorial Universitaria, Santiago, Chile.
- LAURANCE WF & RO BIERREGAARD (1997) Tropical forest remnants. University of Chicago Press, Chicago, Illinois. xv + 616 pp.
- LAWLOR TE (1986) Comparative biogeography of mammals on islands. *Biological Journal of the Linnean Society* 28: 99-125.
- LIDICKER WJ (ed) (1995) Landscape approaches in mammalian ecology. University of Minnesota Press, Minneapolis, Minnesota. ix + 215 pp.
- LOMOLINO MV & DR PERAULT (2000) Assembly and dis-assembly of mammal communities in a fragmented temperate rainforest. *Ecology* 81: 1517-1532.
- LOMOLINO MV & DR PERAULT (2001) Island biogeography and landscape ecology of mammals inhabiting fragmented, temperate rain forests. *Global Ecology and Biogeography* 10: 113-132.
- LYNAM AJ (1997) Rapid decline of small mammal diversity in monsoon evergreen forest fragments in Thailand. In: Laurance WF & RO Bierregaard Jr (eds) *Tropical forest remnants: ecology, management, and conservation of fragmented communities*: 222-240. University of Chicago Press, Chicago, Illinois.
- MALCOLM JR (1997) Biomass and diversity of small mammals in Amazonian forest fragments. In: Laurance WF & RO Bierregaard Jr (eds) *Tropical forest remnants: ecology, management, and conservation of fragmented communities*: 207-221. University of Chicago Press, Chicago, Illinois.
- MCCULLOUGH DR (ed) (1996) Metapopulations and wildlife conservation. Island Press, Washington, District of Columbia. x + 429 pp.
- MESERVE PL & FM JAKSIC (1991) Comparisons of terrestrial vertebrate assemblages in temperate rainforests of North and South America. *Revista Chilena de Historia Natural* 64: 511-535.
- MESERVE PL, BK LANG, R MURÚA, A MUÑOZ-PEDREROS & LA GONZÁLEZ (1991) Characteristics of a terrestrial small mammal assemblage in a temperate rainforest. *Revista Chilena de Historia Natural* 64: 157-169.
- MITTERMEIER RA, N MYERS, JB THOMSEN & GAB DA FONSECA (1998) Biodiversity hotspots and major tropical wilderness areas: approaches to setting conservation priorities. *Conservation Biology* 12: 516-520.

- NUPP TE & RK SWIHART (2000) Landscape-level correlates of small-mammal assemblages in forest fragments of farmland. *Journal of Mammalogy* 81: 512-526.
- OLSON DM & E DINERSTEIN (1998) The Global 200: a representation approach to conserving the Earth's most biologically valuable ecoregions. *Conservation Biology* 12: 502-515.
- PATTERSON BD (1992) A new genus and species of long-clawed mouse (Rodentia: Muridae) from temperate rainforests of Chile. *Zoological Journal of the Linnean Society* 106: 127-145.
- PERAULT DR & MV LOMOLINO (2000) Corridors and mammal community structure across a fragmented, old-growth forest landscape. *Ecological Monographs* 70: 401-422.
- ROBINSON SK, FR THOMPSON III, TM DONOVAN, DR WHITEHEAD & J FAABORG (1995) Regional forest fragmentation and the nesting success of migratory birds. *Science* 267: 1987-1990.
- ROSENBLATT DL, EJ HESKE, SL NELSON, DH BARBER, MA MILLER & B MACALLISTER (1999) Forest fragments in east-central Illinois: islands or habitat patches for mammals? *American Midland Naturalist* 141: 115-123.
- ROSENZWEIG ML (1995) Species diversity in space and time. Cambridge University Press, Cambridge, United Kingdom. xxi + 436 pp.
- ROZZI R, D MARTÍNEZ, MF WILLSON & C SABAG (1995) Avifauna de los bosques templados de Sudamérica. In: Armesto JJ, C Villagrán & MK Arroyo (eds) *Ecología de los bosques nativos de Chile*: 135-152. Editorial Universitaria, Santiago, Chile.
- RUNDEL PW, G MONTENEGRO & FM JAKSIC (eds) (1998) Landscape disturbance and biodiversity in Mediterranean-type ecosystems. *Ecological Studies* 136: 1-447.
- SIEVING KE, MF WILLSON & TL DE SANTO (1996) Habitat barriers to movement of understory birds in fragmented south-temperate rainforest. *Auk* 113: 944-949.
- SIEVING KE, MF WILLSON & TL DE SANTO (2000) Defining corridor functions for endemic birds in fragmented south-temperate rainforest. *Conservation Biology* 14: 1120-1122.
- VUILLEUMIER F (1985) Forest birds of Patagonia: ecological geography, speciation, endemism, and faunal history. *Ornithological Monographs* 36: 255-304.
- VUILLEUMIER F & D SIMBERLOFF (1980) Ecology versus history as determinants of patchy and insular distributions in high Andean birds. *Evolutionary Biology* 12: 235-379.
- WILCOVE DS, CH MCLELLAN & AP DOBSON (1986) Habitat fragmentation in the temperate zone. In: Soulé ME (ed) *Conservation biology*: 237-256. Sinauer Associates Inc., Sunderland, Massachusetts.
- WILLSON MF, TL DE SANTO, C SABAG & JJ ARMESTO (1994) Avian communities of fragmented south-temperate rainforests in Chile. *Conservation Biology* 8: 508-520.

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