

PATTERNS OF SMALL MAMMAL SPECIES RICHNESS IN
MEDITERRANEAN AND TEMPERATE CHILE

PATRONES EN LA RIQUEZA DE ESPECIES DE PEQUEÑOS MAMÍFEROS EN
LAS REGIONES MEDITERRÁNEA Y TEMPLADA DE CHILE

Hernán L. Cofré, Horacio Samaniego, and Pablo A. Marquet

ABSTRACT

While it is widely accepted that species richness and rarity are non-randomly distributed across time, space, and taxa, it is by no means evident which are the factors affecting the distribution patterns of both attributes. In this study we analyze richness and rarity patterns of small mammals (rodents and marsupials) in Mediterranean and Temperate Chile. We test for the effect of environmental factors that may explain richness and endemism variability after accounting for spatial autocorrelation. We also analyze the relationship between species traits and correlates of rarity (density and range size) after accounting for phylogenetic relatedness. Our results show that energy input and to a lesser degree glaciations may explain richness pattern of small mammals from forest habitats in Chile, whereas glaciations and topographic heterogeneity are associated with endemism patterns. Both factors may explain the high richness found at 37° S and the low values at the southernmost tip of the continent. When phylogenetic relatedness was accounted for, the number of vegetation types was the only ecological trait significantly associated with density and latitudinal range. Our results reinforce the importance of energy availability and productivity in determining patterns in biodiversity.

Key words: Chile, diversity, mammals, Mantel test, rarity, macroecology, phylogenetic effects

RESUMEN

Si bien la idea de que la riqueza y la rareza específica tienen una distribución no aleatoria con relación al tiempo, el espacio, y la taxonomía, no es para nada evidente cuáles son los factores que afectan los patrones de distribución de aquellos dos atributos. En este estudio analizamos los patrones de riqueza y rareza de pequeños mamíferos (roedores

y marsupiales) en Chile mediterráneo y templado. Ponemos a prueba el efecto de los factores ambientales en la variación en riqueza y endemismo luego de dar cuenta de la autocorrelación espacial. También analizamos la relación entre rasgos específicos y correlatos de la rareza (densidad y tamaño del rango de distribución) luego de dar cuenta del parentesco filogenético. Nuestros resultados muestran que la cantidad de energía y, en menor grado, el efecto de las glaciaciones, pueden explicar los patrones de riqueza de los pequeños mamíferos en los habitats boscosos en Chile, mientras que las glaciaciones y la heterogeneidad topográfica están asociadas a los patrones de endemismo. Ambos factores pueden explicar la alta riqueza encontrada a 37° S y los bajos valores en el extremo sur del continente. Cuando se tuvo en cuenta el parentesco filogenético, el número de tipos vegetacionales fue el único factor ecológico asociado significativamente con la densidad y el rango latitudinal. Nuestros resultados refuerzan la importancia de la disponibilidad de energía y la productividad en la determinación de los patrones de biodiversidad.

Palabras claves: Chile, diversidad, mamíferos, test de Mantel, rareza, macroecología, efectos filogenéticos

INTRODUCTION

Spatial patterns of variability in species richness have been reported for centuries. Recently, however, they have gained renewed attention, driven by the urgent need to improve our understanding of processes underlying its generation and maintenance (e.g., Ceballos and Brown, 1995; Rosenzweig, 1995; Hubbell, 2001; Blackburn and Gaston, 2003; Gaston, 2003) at local, regional, and global scales (e.g., Ricklefs and Schluter, 1993; Brown, 1995; Gaston 2000). Unfortunately, and despite decades of research, no simple general answer to the question of the determinants of species diversity at any single scale, let alone to explain how the different scales interact to the formation of biodiversity patterns, is yet available (Hubbell, 2001; Whittaker et al., 2001). One way of improving our understanding of factors determining spatial changes in diversity is by expanding the traditional scope of analysis beyond the quantification of species numbers to encompass associated traits such as abundance, geographic range, and body size, and how they may contribute to the observed patterns (Arita and Figueroa, 1999; Kaspari et al., 2000; Jetz and Rahbek, 2002; Marquet et al., 2004; Ruggiero and Kitzberger, 2004; Vázquez and Gaston, 2004). Although this phenomenological approach can be criticized as lacking a solid theoretical foundation and by its limited predictability and generality, it may nevertheless allow us to at least identify those factors that might need to be included and/or accounted for in a general theory of biodiversity.

Numerous studies have assessed species richness, endemism, and rarity across geographical areas in the context of identifying priority areas for the conservation of biodiversity (Prendergrast et al., 1993; Ceballos and Brown, 1995; Williams et al., 1996; Arita et al., 1997; Dobson et al., 1997; Kerr, 1997; Ceballos et al., 1998; Baquero and Tellería, 2001). However, few of these studies have assessed how environmental factors and life history traits affect patterns of species richness and rarity (Ceballos and Brown, 1995; Baquero and Tellería, 2001; Ruggiero and Kitzberger, 2004). On the other hand, rarity has been recognized as an indicator of extinction risk and provides

a concrete basis for identification of threatened species (Diamond, 1984; Rabinowitz et al., 1986; Pimm et al., 1988; Arita et al., 1990; Arita, 1993; Manne et al., 1999; Purvis et al., 2000; Manne and Pimm, 2001; Cardillo et al., 2004). In spite of this, little consensus exists about the factors that best predict species abundance and/or range distribution (Bevill and Louda, 1999; Murray et al., 2002; Gaston, 2003).

In this chapter, we attempt to answer some questions related to the richness and rarity of small mammals from the Mediterranean and Temperate zones of Chile. Specifically, we ask if spatial patterns in the distribution of small mammal species are congruent with the spatial distribution of endemism, and if there is any congruence among the environmental and historical factors that may explain patterns in species richness and rarity.

MATERIALS AND METHODS

Study Area and Taxonomic Group

According to Armesto et al. (1996) native forests in Chile occur between 30° and 55° S. In this gradient of 25 degrees of latitude, we can find two main kinds of forest: Sclerophyllous forest (31° - 36°) and Temperate rain forest (36° - 55°) (see also Armesto et al., 1996; Amigo and Ramírez 1998). In the Mediterranean region (mostly Sclerophyllous forests), mean annual precipitation ranges between 200 and 1000 mm and occurs mostly in winter. The average annual maximum temperature ranges between 12° and 16°C, and the minimum is rarely below 0°C. On the other hand, the Temperate region experiences mean annual rainfall from 800 to 4000 mm, and average annual maximum temperatures between 7° and 14°C (Di Castri and Hajek, 1976; Amigo and Ramírez, 1998).

Our study area extends from 30° to 55° S and from sea level to 2500 m. We used a geographic information system (GIS) to divide the study area to 274 half-degree quadrants. We selected 50 quadrants that satisfied the requirements of being located only in the Sclerophyllous or Temperate forest ecoregions, and not overlapping with the Patagonian or Andean steppe ecoregions. This general approach has been widely used in a broad range of ecological studies to map species richness (e.g. Arita et al., 1990, 1997; Kerr and Packer, 1997; Ceballos et al., 1998; Baquero and Telleria, 2001; Hawkins and Porter, 2003; Rodríguez and Arita, 2004; Ruggiero and Kitzberger, 2004; Tognelli and Kelt, 2004). Our species pool includes 33 small mammal species (<500 g) inhabiting forest in Mediterranean and Temperate zones of Chile (Table 1). Taxonomy follows Yañez and Muñoz-Pedreros (2000), although we consider *Abrothrix xanthorhinus* to be a junior synonym of *A. olivaceus* following Smith et al. (2001).

Variables and Statistical Methods

Variables. The dependent variables in all diversity analyses were species richness and endemism. Species richness was determined by tallying the number of species whose geographic range overlapped each half-degree quadrant. Endemism was quantified using the following index:

Table 1. Small mammals species found in forest habitats in Mediterranean and Temperate Chile. Type of forest: MF = Mediterranean forest, TF = Temperate forest.

Family	Species	Type of forest
Didelphidae	<i>Thylamys elegans</i>	mainly MF / marginally TF
Caenolestidae	<i>Rhyncholestes raphanurus</i>	TF
Microbiotheriidae	<i>Dromiciops gliroides</i>	Marginally MF / mainly TF
Muridae	<i>Oligoryzomys longicaudatus</i>	MF / TF
	<i>Oligoryzomys magellanicus</i>	TF
	<i>Akodon herskovitzi</i>	TF
	<i>Akodon lanosus</i>	TF
	<i>Akodon markhami</i>	TF
	<i>Abrothrix olivaceus</i>	MF / TF
	<i>Abrothrix sanborni</i>	TF
	<i>Abrothrix longipilis</i>	MF / TF
	<i>Geoxus valdivianus</i>	marginally MF / mainly TF
	<i>Chelemys megalonyx</i>	MF
	<i>Chelemys macronyx</i>	marginally TF
	<i>Pearsonomys annectens</i>	TF
	<i>Phyllotis darwini</i>	MF / marginally TF
	<i>Phyllotis xanthopygus</i>	marginally TF
	<i>Loxodontomys pikumche</i>	marginally MF
	<i>Loxodontomys micropus</i>	TF
	<i>Irenomys tarsalis</i>	marginally MF / TF
	<i>Reithrodon physodes</i>	marginally TF
	<i>Euneomys chinchilloides</i>	marginally TF
Chinchillidae	<i>Chinchilla lanigera</i>	marginally MF
Octodontidae	<i>Octodon degus</i>	MF
	<i>Octodon bridgesi</i>	MF / TF
	<i>Octodon lunatus</i>	MF
	<i>Octodon pacificus</i>	TF
	<i>Spalacopus cyanus</i>	MF
	<i>Aconaemys fuscus</i>	TF
	<i>Aconaemys sagei</i>	TF
	<i>Aconaemys porteri</i>	TF
Ctenomyidae	<i>Ctenomys maulinus</i>	marginally MF/TF
Abrocomidae	<i>Abrocoma bennetti</i>	MF

$$I_e = \frac{\sum_{i=1}^{n_s} 1/R_i}{n_s}$$

where R_i represents the latitudinal range for species i (Gaston, 1994) and n_s corresponds to the total number of species per site (s). This type of index has been used to study patterns of congruence in the spatial distribution of endemism and species richness (e.g., Williams et al., 1996; Arita et al., 1997; Baquero and Tellería, 2001). However, we also use it to evaluate the relationship between endemism and environmental variables. In order to assess the effect of the environment on species richness we considered 6 environmental variables for each quadrant: the normalized difference vegetation index (NDVI), the mean Elevation (Elevation), the mean daily temperature (Temperature), mean daily precipitation (Precipitation), the number of vegetation types (Vegetation Types), and the history of Glaciation. This last variable is a binary variable that indicates whether or not a quadrant was covered by ice during the last glacial maximum (Mercer, 1983; see also Vuilleumier, 1971; Villagrán et al., 1996). NDVI is a measure of “greenness” that is obtained from images developed by the National Oceanic and Atmospheric Administration’s Advanced Very High Resolution Radiometer satellite (NOAA AVHRR). NDVI appears to correlate strongly with plant biomass, primary productivity, and actual evapotranspiration (e.g., Box et al., 1989; Hobbs, 1995; Paruelo et al., 1998, 2001) and has been broadly used as a surrogate of productivity in studies of avian and mammal diversity (Fraser, 1998; Acevedo and Currie, 2003; Hurlbert and Haskell, 2003; Hawkins, 2004; Hurlbert, 2004; Tognelli and Kelt 2004). The NDVI data used here corresponds to the mean value (from April 1992 to March 1993) for each half-degree quadrant and was obtained from <http://edcsns17.cr.usgs.gov/1KM/>. The same procedure was used to obtain the mean elevation based on 30 arc-second map produced by the United States Geological Survey (available at http://edcdaac.usgs.gov/gtopo30/hydro/sa_dem.asp). Mean daily temperature and mean daily precipitation were obtained from the 1961-1990 databases available at the IPCC Data Distribution Center (<http://ipcc-ddc.cru.uea.ac.uk>). The number of vegetation types in each quadrant was obtained by counting the variety of vegetation types in each quadrant following Gajardo (1994).

To assess the relationship between rarity and life-history traits, species were classified according to body size, mean litter size, diet, habitat breadth, activity period (diurnal vs. nocturnal), life form or habit (terrestrial vs. fossorial), and sociability (social vs. non-social). We defined rarity based on density and range size of species (Gaston 1994). We compiled data on density, latitudinal range, diet, body mass, habitat use, and life history traits using published literature (e.g., Mann, 1978; Pearson and Pearson, 1982; Pearson, 1983, 1984; Reise and Venegas, 1987; Johnson et al., 1990; Meserve and Jaksic, 1991; Meserve et al., 1991; Jiménez et al., 1992; Redford and Eisenberg, 1992; Kelt, 1994; Murúa, 1996; Spotorno et al., 1998, 2001; Cofré and Marquet, 1999; Muñoz and Yañez, 2000; Saavedra and Simonetti, 2000, 2001, 2003; Ebersperger and Cofré, 2001). Density of each species was defined as the mean of values reported in the literature. The geographic range of each species was defined by latitudinal extent (*sensu* Gaston, 1994; see also Gillespie, 2002). Habitat breadth was assessed by counting the occurrence of each species in different types of habitat. We followed Murúa (1996) for most species habitat occurrences. For species endemic to the Mediterranean region, habitat occurrence was assigned by a literature review

(Mann, 1978; Jaksic, 1997; Muñoz and Yañez, 2000 and reference therein). We then tallied the number of vegetation types in which each species may be found. To analyze the role of trophic status we created 2 dummy variables (Draper and Smith, 1998; Zar, 1999) – herbivory and insectivory; based on published studies, all species were characterized as herbivore (“herbivory” = 1, “insectivory” = 0), omnivore (“herbivory” = 1, “insectivory” = 1), or insectivore (“herbivory” = 0, “insectivory” = 1). Habits were defined as either terrestrial or fossorial. Mean body mass (g), latitudinal range size, and litter size were \log_{10} transformed for all statistical analyses. Density was expressed as \log_{10} (mean regional density +1).

Statistical Analyses. To explore the univariate relationship between rarity and species attributes, we applied regression analysis or ANOVA, depending on trait type. To assess the extent to which the observed variance in density and latitudinal range may be explained by a combination of species’ attributes we applied a multiple regression analysis with backward elimination and stepwise forward selection methods (Zar, 1999). In the backward procedure, the least significant variables were removed until 2 criteria were met: first, explained variance (R^2) was maximal, and second, all the variables in the model were significant ($p < 0.1$; Draper and Smith, 1998; Zar, 1999). Variables already in the model that lost their significance during the process were deleted. The stepwise forward selection procedure was stopped when no remaining variable was significant ($p < 0.1$), if added to the model. Both analyses were performed separately, and we selected the model (forward vs. backward procedure) which explained the greatest amount of variance. Because multiple regressions may fail to identify significant independent variables when multicollinearity is present, we examined the tolerance values in this procedure. Tolerance is computed as $1 - R^2$ for a regression between a given independent variable and all other independent variables (Legendre and Legendre, 1998; Draper and Smith, 1998; Zar, 1999; Graham, 2003). As a rule of thumb, multicollinearity is indicated by tolerance values < 0.20 . In this study, all tolerance values were > 0.5 ; therefore all variables had a small redundancy or large contribution to the regression.

Because our analysis involves comparisons across different species, it is possible that species can share traits because of shared ancestry (Felsenstein, 1985; Harvey and Pagel, 1991). To assess the contribution of phylogenetic relatedness on traits potentially associated to rarity, we used the Signed Mantel test (Böhning-Gaese et al., 2000; Böhning-Gaese and Oberrath, 2001; Oberrath and Böhning-Gaese, 2002), which is an extension of the traditional Mantel test (Mantel, 1967; Smouse et al., 1986; Legendre et al., 1994; Taylor and Gotelli, 1994). A Mantel test assesses the correlation between the elements of 2 distance matrices (Manly, 1986). To construct each matrix, each trait x species combination is compared with all the other species. Thus, for each variable (dependent and independent), the distance data on N sampling units (small mammal species) are represented by an $N \times N$ matrix with $N(N - 1) / 2$ different paired distances. We constructed two \mathbf{Y} matrices describing the dissimilarity (distance) in regional density and latitudinal range, respectively, an \mathbf{X}_1 matrix with the phylogenetic distance among species (= taxonomic distance; Oberrath and Böhning-Gaese 2002), and $\mathbf{X}_2 \dots \mathbf{X}_n$ matrices representing the dissimilarities in the other attributes among species. The Mantel test determines the statistical relationship between these matrices. In the univariate version of the test each of the matrices representing the predictor variables were assessed separately. For the multivariate analysis we used the same

independent predictor variables as identified by the multiple regression procedure. In Mantel tests, the regression of the individual values in the matrices yields the partial regression coefficients b_1 and b_{2n} and the respective t -values (Smouse et al., 1986). A valid significance level for each variable (the Mantel significance level) is then derived by comparing the original t -value with a null distribution of t -values constructed by Monte Carlo randomization. For each permutation, the X_1 and $X_{2,\dots,n}$ matrices are held constant and the species in the Y matrix are randomly permuted (Smouse et al., 1986; Oberrath and Böhning-Gaese, 2001). To construct the null distribution of t -values we used 2000 randomizations.

To study the univariate relationship between community traits (endemicity and richness) and environmental variables, we also applied Poisson or linear regression analyses for richness and endemicity respectively. In multivariate models for species richness and endemicity we examined the extent to which the observed variance may be explained by only two historical or environmental variables to avoid the effect of multicollinearity and overfitting (e.g. Currie and Fritz 1993; Van Rensburg et al., 2002). Model selection was based on the Akaike Information Criterion (Akaike 1973). For simple and multiple Poisson regression analyses, model fit was assessed by analyzing the deviance table using a Chi-square approximation (Dalgaard 2002) in the R statistical software (R Development Core Team 2005). In the multivariate analysis of endemicity, the dichotomous variable Glaciation was entered as a dummy variable.

To test for the potential effect of spatial autocorrelation and properly control for its effect on environmental and community traits (endemicity and richness) we again employed the Signed Mantel test (Legendre and Legendre, 1998; Oberrath and Böhning-Gaese, 2001; Lemoine and Böhning-Gaese, 2003). We constructed two dissimilarity Y matrices (as distances of richness and endemicity index, respectively), an X_1 matrix with the spatial distance among sites, and $X_{2,\dots,n}$ matrices representing dissimilarities in environmental traits. Valid significance levels for each X-variable (the Mantel significance level) were derived by comparing the original t -value with a null distribution of t -values obtained from 2000 Monte Carlo randomizations (Oberrath and Böhning-Gaese, 2001). Geographic distance between sites was calculated using the Great-Circle distance calculator available in the Fields package (Nychka 2004) of the R statistical software (R Development Core Team 2005).

When necessary, variables were transformed to be as close to normality as possible. Specifically, Temp was \log_{10} transformed and NDVI, Number of vegetation types, and Elevation were square root transformed. Unless stated otherwise, all regular statistical methods were implemented with Statistica 5.1 for Windows (StatSoft Inc., Tulsa, Oklahoma, USA).

RESULTS

Richness, Endemicity, and Environmental traits

Species richness showed the classic latitudinal pattern with a monotonic decrease from high values at low latitudes to low values at high latitudes (Fig. 1a). Nevertheless, the highest richness values were found between 35° and 40° S (see also spatial patterns in Fig. 2). On the other hand, the endemicity index shows a decreasing trend from 30° to 50° S punctuated by peaks at 38° and 52° S and a steep increase at the tip of the

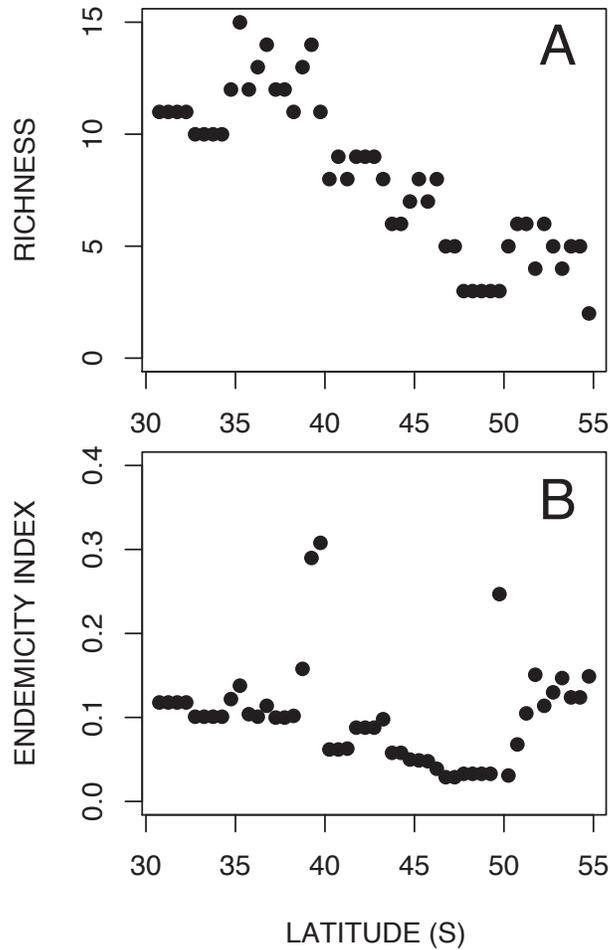


Figure 1. Mammal species richness (a) and endemism (b; I_e) in each 0.5° (lat/long) quadrant, as a function of latitude, in Mediterranean and Temperate Chile (30° - 55° S).

continent (Fig. 1b; see also Fig. 2).

Univariate analyses show that all 6 environmental and historical variables were statistically associated with species richness (Table 2). NDVI, Temperature, and Glaciation showed the strongest relationship with richness (i.e., large deviance and low AIC; see also Fig. 3). Endemism also showed a strong association with all environmental and historical variables (Table 2), but with the number of vegetation types. Elevation, Temperature, and Glaciation were the variables that best predicted endemism (Fig. 4).

The best 2-variable regression model for species richness variation included the positive effects of NDVI and Temperature (Table 3) a measure of productive energy available for consumers and of solar energy availability respectively (Evans et al.

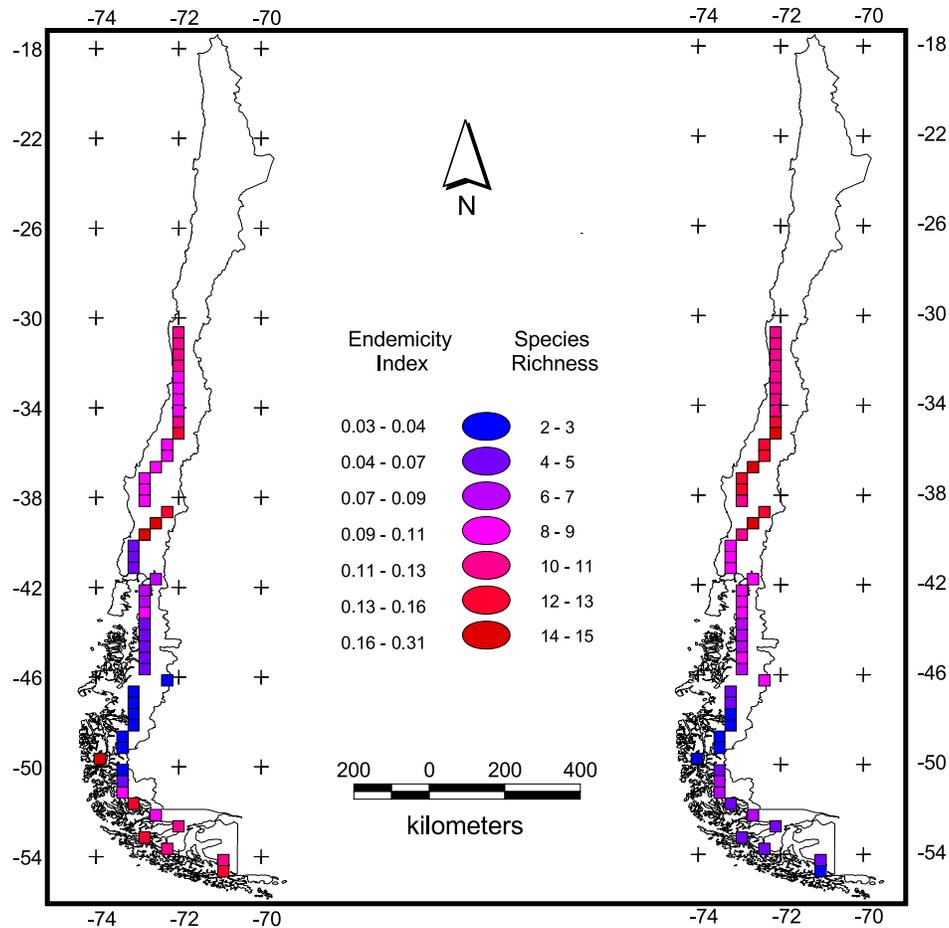


Figure 2. Spatial distribution of mammal species richness and endemism (Ie) in Mediterranean and Temperate Chile. Maps of Chile are superimposed by a grid of 49 0.5° (lat/long) quadrats.

2005). In the case of endemism, the best model included Elevation and Glaciation. In this case non-glaciated areas had a larger endemism index than glaciated ones (Table 3).

The signed Mantel test results (Table 4) show a significant effect of Temperature and NDVI on richness and of Elevation and Glaciation in endemism. It also reveals that there is a significant influence of spatial autocorrelation on richness. This was apparent in a significant effect of geographic distance and an increase in explained variability in richness in the two variable model when distance was included. Endemism, however, was not affected by spatial autocorrelation.

Rarity and Life-history Traits

Without taking phylogenetic relatedness among species into account, univariate analyses show that latitudinal range and mean density are similarly influenced by

Table 2. Univariate analyses to assess the influence of six predictor variables on species richness (using Poisson regression) and endemism (using linear regression) of small mammals assemblages in Mediterranean and Temperate Chile.

Predictor Variables	Regional richness		Endemism Index		
	Deviance	AIC	Coefficient	F value	AIC
NDVI	52.03***	216.2	0.44	11.56**	-1.28
Elevation	10.23**	258	-0.57	22.55**	-9.71
Vegetation types	30.69***	237.5	0.25	3.16 n.s	6.3
Temperature	57.35***	210.9	0.45	12.04**	-1.68
Precipitation	15.98***	252.2	-0.35	6.71**	2.95
Glaciation	48.09***	220.14	-0.23	11.74**	-1.43

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

species attributes (Table 5). Latitudinal range and density were significantly and positively correlated with the number of vegetation types, such that specialists (i.e., species found in quadrants with few vegetation types) not only have narrower geographic ranges, but also occur at lower densities than do generalists (Fig. 5). The multivariate regression analysis gave results similar to the univariate analysis (Table 6). For density, the variables that entered the model were number of vegetation types (a measure of habitat breadth) and habits (terrestrial vs. fossorial). Similarly, the latitudinal range of species was best predicted by the number of vegetation types and by herbivory.

Phylogeny did not have a significant effect on density or geographic range (Table 6). When phylogenetic relatedness was accounted for, the results did not change, and the number of vegetation types remained as the only ecological trait significantly associated with latitudinal range and vegetation types and habits were the only traits related with density.

DISCUSSION

Richness, Endemism and Environmental traits

In this work, we have documented patterns of species richness for small mammals inhabiting forested habitats in Chile. Species richness is highest between 35° and 40° S, followed by a decrease in richness until the tip of the continent. This non-linear pattern has also been reported in plants (Villagrán, 1995; Arroyo et al., 1996), birds (Cofré, 2004), and butterflies (Samaniego and Marquet, unpubl. data). Our results suggest that this pattern may be driven by ecological factors associated with energy input, as measured by NDVI and temperature. Similar results have been reported recently for the South American mammal fauna (Ruggiero and Kitzberger, 2004; Tognelli and Kelt, 2004) at a continental scale; these authors found that variables associated with productivity, such as actual evapotranspiration, NDVI, and solar radiation were the most important in affecting spatial changes in species richness for mammals. However,

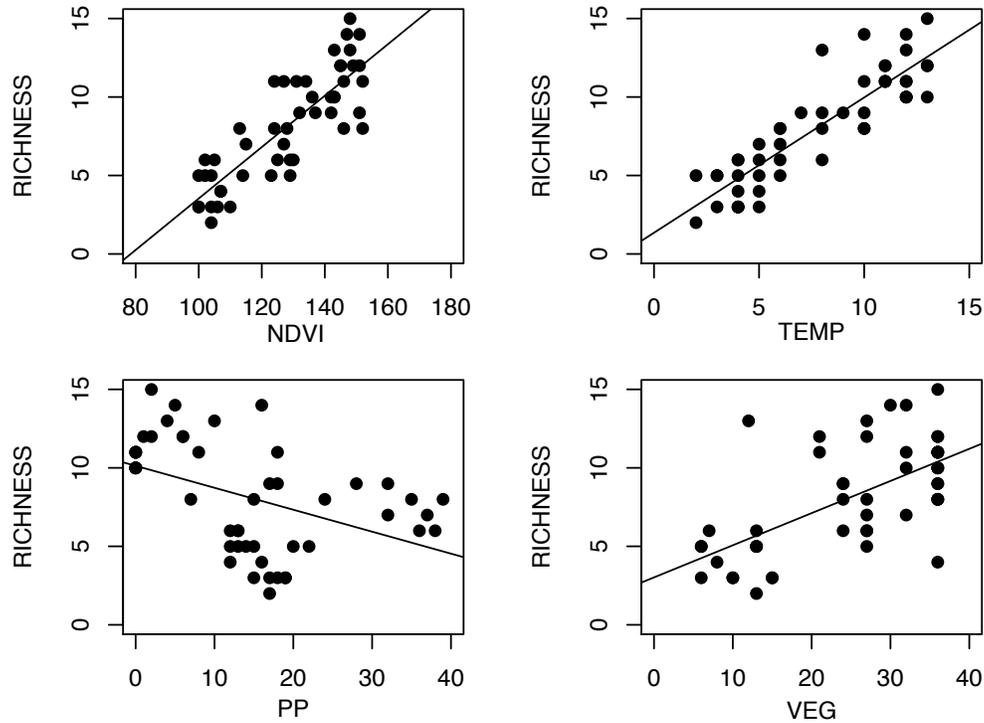


Figure 3. Mammal species richness in each 0.5° (lat/long) quadrat as a function of NDVI ($r_s = 0.81$, $p < 0.0001$); temperature ($r_s = 0.87$, $p < 0.0001$); annual mean daily precipitation, ($r_s = -0.54$, $p < 0.001$); and number of vegetation types ($r_s = 0.58$, $p < 0.001$).

we also found that glacial events may play a role in explaining richness patterns. Glaciation was the third most important determinant of richness in univariate analysis and strongly affected the spatial pattern of endemism. It has been recently recognized that Pleistocene refuges and non-glaciated areas in the Nearctic and Palearctic can explain current biodiversity patterns as they have acted as important diversification centers (e.g., Mönkkönen and Viro, 1997; Baquero and Telleria, 2001; Hawkins and Porter, 2003). On the other hand, we also found a tendency for glaciated sites to exhibit lower endemism indices than non-glaciated sites. This indicates that species with smaller ranges are not represented in most of the glaciated sites (see also Mönkkönen and Viro, 1997; Baquero and Telleria, 2001; Hawkins and Porter, 2003). According to Vuilleumier (1971), the main effect of Quaternary glaciations has been the reduction of species distribution in glaciated areas south of 45° S. Further analyses, however, are needed to substantiate the effect of glaciations and to separate them with others, such as a potential peninsular effect.

The lower regional richness observed between 45° and 52° S coincides with low endemism, given the over-representation of species with broad ranges from the Mediterranean area (e.g., *Abrothrix longipilis*, *A. olivaceus*) or other biomes (e.g., *Euneomys chinchilloides*, *Phyllotis xanthopygus*) (Murúa, 1996). We also observed a peak

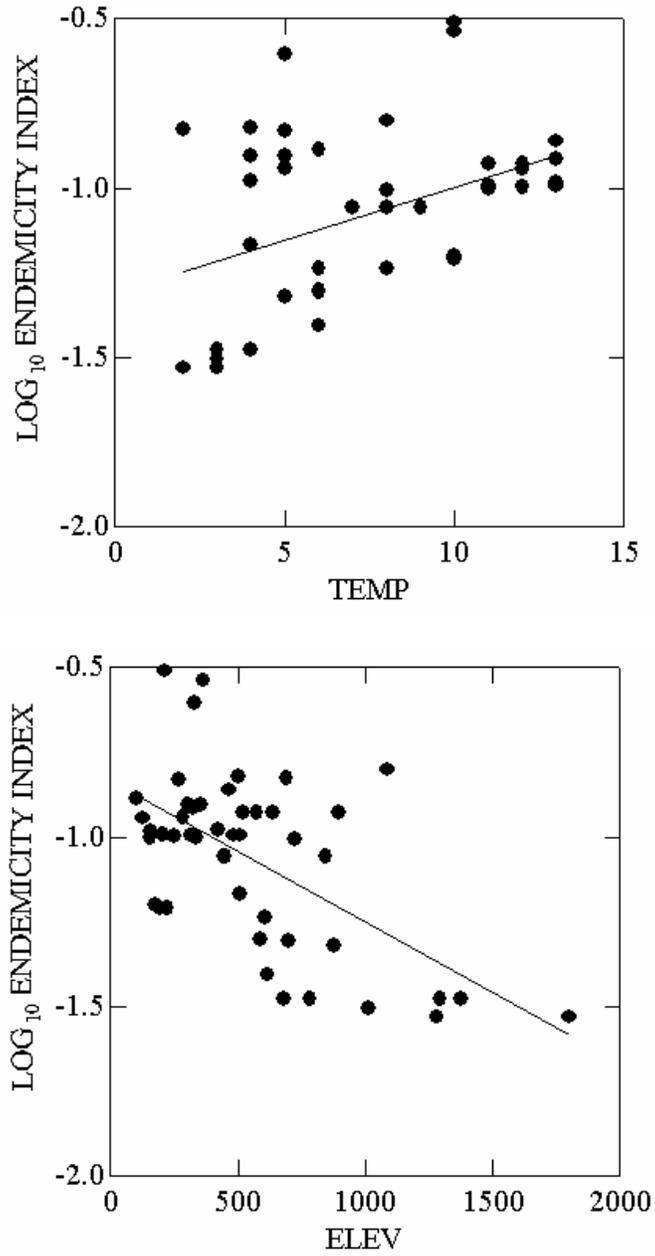


Figure 4. Mammal endemism (I_e) as a function of temperature ($r_s = 0.34, p < 0.02$) and mean elevation ($r_s = -0.45, p < 0.001$).

Table 3. Best two variable model for species richness (based on Poisson regression) and endemicity (based on linear multiple regression) of small mammals assemblages in Mediterranean and Temperate Chile.

Richness				Endemicity			
Predictor Variables	Coefficient	Deviance	AIC	Predictor Variables	Coefficient	R ²	AIC
Temperature	1.31	57.35***	11.33	Elevation	-0.01***	0.36	-12.34
NDVI	0.17	1.55 n.s		Glaciation	-0.14*		

*** $p < 0.001$, * $p < 0.05$

Table 4. Results of multivariate Signed Mantel test including and not including spatial autocorrelation when testing for the influence of environmental variables on species richness and endemicity. Numbers are partial correlations.

Models with Environmental Variables	Richness		Endemicity	
	not including geographic distance	including geographic distance	not including geographic distance	including geographic distance
Temperature	12.75***	3.94**		
NDVI	9.06***	11.11***		
Distance		12.09***		
R ²	0.48	0.55		
Elevation			-14.16***	-14.12***
Glaciation			-7.93***	-7.98***
Distance				0.98 n.s.
R ²			0.24	0.20

** $p < 0.01$, *** $p < 0.001$

in endemism at the bottom of the latitudinal gradient due to species with restricted insular distributions (e.g., *Akodon lanosus*, *A. hershkovitzi*, *A. markhami*, and *Oligoryzomys magellanicus*). These species likely diversified in this area after it was colonized by ancestral taxa coming from more northern areas when Pleistocene ice fields started to retreat (e.g., Smith et al., 2001; Palma et al., 2005).

Biogeographic studies using unprojected latitudinal bands or degree-based quadrants are likely to be affected by area, as the area at different latitude differ due to the poleward convergence of longitudinal meridians (e.g., Lyons and Willig, 1999, Romdal et al., 2005). Area has no effect on richness in our study, probably because of the short latitudinal extent included in the analysis. This claim is based on the fact that none of all possible 2-variable models including area as a predictor had lower AIC value than the best model reported in Table 3. The same result has been observed when

Table 5. Results of univariate analyses (linear regression or one-way ANOVA) on the influence of eight species attributes either on the \log_{10} density or the \log_{10} latitudinal range of small mammal species from Mediterranean and Temperate Chile.

Variable	\log_{10} Density		\log_{10} Latitudinal range	
	Slope	F value	Slope	F value
Body size	-0.02	0.01	-0.25	2.09
Herbivory		0.51		0.66
Insectivory		0.003		0.11
Number of vegetation types	0.45	5.75*	0.61	18.17***
Activity		3.45		0.41
Habits		0.42		0.85
Sociability		0.21		0.05
Litter size	0.04	0.02	0.19	0.61

* $p < 0.05$, *** $p < 0.001$

analyzing all mammalian species in half-degree quadrants across Chile (Samaniego and Marquet, unpublished data.)

We have also shown a significant and positive effect of topographic heterogeneity on endemism, as measured by mean difference in elevation. Such topographic heterogeneity may increase isolation between populations, and may foster population differentiation and speciation processes, thereby increasing the diversity of these areas, as suggested by Fuentes and Jaksic (1979) for lizards.

Rarity and Life-history Traits

At least 10 different hypotheses have been proposed to explain species rarity (see reviews by Kunin and Gaston, 1993; Gaston and Kunin, 1997; Gaston, 2003). We have found a strong relationship between latitudinal range and the number of vegetation types, or habitat breadth. We also find significant associations between density and number of vegetation types. Small mammals that only occur in a few habitats in Mediterranean or Temperate Chile have a significantly smaller latitudinal extent and a smaller population density than widespread mammals that occur in many habitats. This is in agreement with Brown's (1984, 1995) niche breadth hypothesis, which states that species with broad niches (e.g., habitat generalists) have higher abundance and larger geographic ranges than species with more restricted niches (e.g., specialists), although the mechanistic basis for this hypothesis might still be questionable, unless an independent measure of niche breadth is used. While a positive relationship between habitat breadth and geographic range has been found for many organisms including mammals (e.g., Jones, 1997; Eeley and Foley, 1999; Harcourt and Coppeto, 2002; see also Gaston, 2003), a correlation between habitat breadth and abundance has not often been reported (see Gaston et al., 1997 for review). However, our results

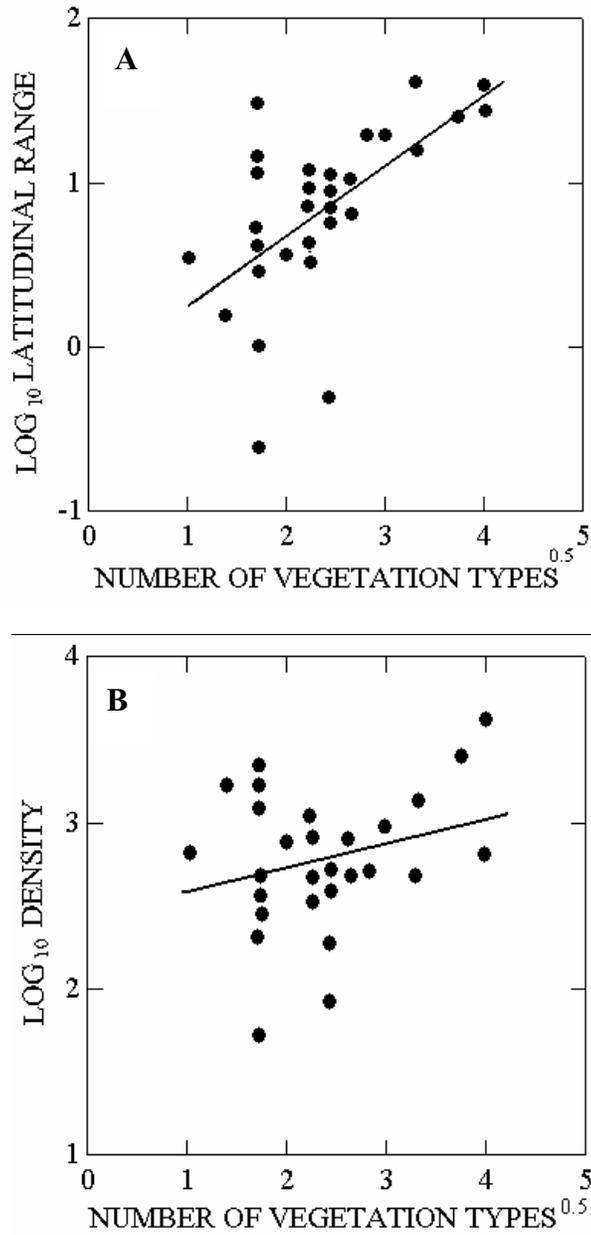


Figure 5. The relationship between number of vegetation types in 0.5° (lat/long) quadrants and latitudinal range (A) and population density (B).

Table 6. Results of multivariate Mantel test with and without consideration of phylogenetic distance, testing the influence of species attributes on \log_{10} Density and \log_{10} of latitudinal range. Numbers in table are t -values.

Species traits	\log_{10} Density		\log_{10} Latitudinal range	
	not including phylogenetic distance	including phylogenetic distance	not including phylogenetic distance	including phylogenetic distance
Phylogeny		0.21		-0.95
Number of Vegetation types	6.06**	6.01**	8.64***	8.63***
Habits	4.55**	4.54**		
R^2	0.13	0.13	0.14	0.14

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

should be interpreted with caution, since our analysis suffers from being restricted to “small mammals” which renders, for example, any correlation between body size and abundance or distribution difficult to find because of the reduced range of the size axis. Since other relationships can be similarly affected, further studies on the complete assemblage of Chilean mammals are necessary to assess the generality of these results.

Conservation Implications

Many studies have found no congruence between the number of rare species and overall richness for mammals (Ceballos and Brown, 1995; Ceballos et al., 1998; Baquero and Tellería, 2001) or other taxa (Prendergrast et al., 1993; Williams et al., 1996; Dobson et al., 1997; Kerr 1997; but see Arita et al., 1997). In contrast, we documented a positive correlation between richness and endemism in small mammals of the Mediterranean and Temperate regions of Chile ($r = 0.628$, $p < 0.001$). This pattern emerges because the majority of the 14 species with the most restricted distributions in this region have their southern or northern distributional boundaries around 37° S. The transitional character of this area contributes to the emergence of this biodiversity pattern (Fig. 1b). For example, Reise and Venegas (1987) described an assemblage of 10 species – including 4 species with their northern distributional boundaries here: *Aconaemys fuscus*, *Ctenomys maulinus*, *Dromiciops gliroides*, and *Loxodontomys micropus* (= *Auliscomys micropus*) near Termas de Chillán ($71^\circ 25' W$, $36^\circ 54' S$, 1,250 m). On the other hand, in coastal forests such as Nahuelbuta National Park ($73^\circ 07' W$, $37^\circ 53' S$, 1,000 m) it is possible to find species from the Mediterranean as well as Temperate forest (e.g., *O. bridgesi* and *P. darwini* are from the Mediterranean area whereas *A. fuscus* and *D. gliroides* belong to the Temperate forest) (Jimenez et al., 1991; see also Fuentes and Jaksic 1979; Reise and Venegas, 1987; Medel et al., 1990; Murúa, 1996).

Species in different rarity categories (sensu Rabinowitz et al., 1986) require different conservation strategies (Arita et al., 1990). For example, specialized species with restricted distribution ranges that overlap species-rich areas (e.g., the genus *Aconaemys*, *Ctenomys maulinus*, *Loxodontomys pikumche*, *Octodon bridgesi*, and *Abrothrix sanborni*) are

likely to benefit from a conservation strategy that targets species-rich regions. On the other hand, restricted and/or low abundance species whose geographic distribution do not overlap species-rich areas (such as *Octodon lunatus*, *Chinchilla lanigera*, *Chelemys megalonyx*, *Pearsonomys annectens*, *Octodon pacificus*, and *Rhyncholestes raphanurus*) will benefit most from a conservation strategy focusing on individual species. Thus, conservation strategies should remain flexible in the face of the diversity of biological attributes exhibited by taxa and habitats.

ACKNOWLEDGMENTS

We acknowledge support from grant FONDAP-FONDECYT 1501-001 and ICM-P05-002. This study was partially funded by a CONICYT fellowship to the senior author. H. Samaniego thanks NSF Biocomplexity grant to J. H. Brown (DEB-0083422) for support. We thank Douglas Kelt for the invitation to participate in this book, and for providing several comments and useful criticisms to improve several drafts of this manuscript. Sos Grande Doug!. We also appreciate the comments made by 2 anonymous reviewers. This is contribution #7 to the Ecoinformatics and Biocomplexity Unit.

LITERATURE CITED

- Acevedo, D., and D. J. Currie
2003 Does climate determine broad-scale patterns of species richness? A test of the causal link by natural experiment. *Global Ecology and Biogeography* 12:461-473.
- Akaike, H.
1973 Information theory as an extension of the maximum likelihood principle. Pp. 267-281 in 2nd International Symposium on Information Theory (Petrov, B. N., and F. Csaksi, eds.). Akademiai Kiado, Budapest, Hungary.
- Amigo, J., and C. Ramírez
1998 A bioclimatic classification of Chile: woodland communities in the temperate zone. *Plant Ecology* 136:9-26.
- Arita, H. T.
1993 Rarity in Neotropical bats: correlations with phylogeny, diet, and body mass. *Ecological Applications* 3:506-517
- Arita, H. T., and F. Figueroa
1999 Geographic patterns of body-mass diversity in Mexican mammals. *Oikos* 85:310-319.
- Arita, H. T., F. Figueroa, A. Frisch, P. Rodríguez, and K. Santos-Del-Prado
1997 Geographical range size and the conservation of Mexican mammals. *Conservation Biology* 11:92-100.

- Arita, H. T., J. G. Robinson, and K. H. Redford
1990 Rarity in Neotropical forest mammals and its ecological correlates. *Conservation Biology* 4:181-192.
- Armesto, J. J., Villagrán, C., and M. T. K. Arroyo (eds.)
1996 *Ecología de los Bosques Nativos de Chile*. Editorial Universitaria, Universidad de Chile, Santiago, Chile.
- Arroyo M. T. K., L. Cavieres, A. Peñaloza, M. Riveros, and A. M. Faggi.
1996 Relaciones fitogeográficas y patrones regionales de riqueza de especies en la flora del bosque lluvioso templado de Sudamérica. Pp. 71-100 in *Ecología de los Bosques Nativos de Chile* (Armesto, J. J., C. Villagrán, and M. T. K. Arroyo, eds.). Editorial Universitaria, Universidad de Chile, Santiago, Chile.
- Baquero R. A., and J. L. Tellería
2001 Species richness, rarity and endemism of European mammals: a biogeographical approach. *Biodiversity and Conservation* 10:29-44.
- Bevill, R. L., and S. M. Louda
1999 Comparisons of related rare and common species in the study of plant rarity. *Conservation Biology* 13:493-948.
- Blackburn, T., and K. J. Gaston (eds.)
2003 *Macroecology: Concepts and Consequences*. Blackwell Publisher, Oxford, UK. 377 pp.
- Böhning-Gaese, K., Halbe, B., Lemoine, N., and R. Oberrath
2000 Factors influencing the clutch size, number of broods and annual fecundity of North American and European land birds. *Evolutionary Ecology Research* 2:823-839.
- Böhning-Gaese, K., and R. Oberrath
2001 Which factors influence the abundance and range size of central European birds? *Avian Science* 1:43-54.
- Box, E. O., B. N., Holben, and V. Kalb
1989 Accuracy of the avhrr vegetation index as a predictor of biomass, primary productivity and net CO₂. *Vegetatio* 80:71-89.
- Brown, J. H.
1984 On the relationship between abundance and distribution of species. *American Naturalist* 124:255-279
1995 *Macroecology*. University of Chicago Press, Chicago, Illinois, USA. 269 pp.

Cofré et al.: Small Mammal Species Richness in Chile

- Cardillo, M., A. Purvis, W. Sechrest, J. L. Gittleman, J. Bielby, and G. M Mace
2004 Human population density and extinction risk in the world's carnivores. *PLoS Biology* 2:0909-0914 (online at <http://biology.plosjournals.org/perlserv/?request=index-html&issn=1545-7885>).
- Ceballos, G., and J. H. Brown
1995 Global patterns of mammalian diversity, endemism, and endangerment. *Conservation Biology* 9:559-568.
- Ceballos, G., P. Rodriguez, and R. A. Medellín
1998 Assessing conservation priorities in megadiverse Mexico: mammalian diversity, endemism and endangerment. *Ecological Application* 8:8-17.
- Cofré, H., and P. A. Marquet
1999 Conservation status, rarity and geographic priorities for conservation of Chilean mammals: An assessment. *Biological Conservation* 88:53-68.
- Cofré, H. L.
2004 Diversidad de Aves en los Bosques del Centro y Sur de Chile: Una Aproximación Macroecológica. Ph.D. Thesis. P. Universidad Católica de Chile, Santiago, Chile.
- Currie, D. J., and J. T. Fritz
1993 Global patterns of animal- and plant- species richness. *Oikos* 67:56-68.
- Dalgaard P.
2002. *Introductory Statistics with R*. Springer-Verlag, New York, New York, USA. xv+267 pp.
- Diamond, J. M.
1984 "Normal" extinctions of isolated populations. Pp. 191-246 in *Extinctions* (Nitecki, M. H., ed.). University of Chicago Press, Chicago, Illinois, USA.
- Di Castri, F., and E. Hajek
1976 *Bioclimatología de Chile*. Pontificia Universidad Católica, Santiago, Chile. 128 pp.
- Dobson, A. P., J. P. Rodríguez, W. M. Roberts, and D. S. Wilcove
1997 Geographic distribution of endangered species in the United States. *Science* 275:550-553.
- Draper, N. R., and H. Smith
1998 *Applied Regression Analysis*. 3rd ed. Wiley, New York, USA. 706 pp.

- Ebensperger, L., and H. Cofré
 2001 On the evolution of group-living in the New World cursorial hystricognath rodents. *Behavioral Ecology* 12:227-236
- Eeley, H. A. C., and R. A. Foley
 1999 Species richness, species range size and ecological specialisation among African primates: geographical patterns and conservation implications. *Biodiversity and Conservation* 8:1033-1056.
- Evans, K. L., P. H. Warren, and K. J. Gaston
 2005 Species-energy relationships at the macroecological scale: a review of the mechanisms. *Biological Reviews* 80:1-25.
- Felsenstein, J.
 1985 Phylogenies and the comparative method. *American Naturalist* 125:1-15
- Fraser, R. H.
 1998 Vertebrate species richness at the mesoscale: relative roles of energy and heterogeneity. *Global Ecology and Biogeography Letters* 7:215-220.
- Fuentes, E. R., and F. M. Jaksic
 1979 Lizard and rodent: an explanation for their relative species diversity in Chile. *Archivos de Biología y Medicina Experimental* 12:179-190.
- Gajardo, R.
 1994 *La Vegetación Natural de Chile. Clasificación y Distribución geográfica.* Editorial Universitaria. Santiago, Chile. 165 pp.
- Gaston, K. J.
 1994 *Rarity.* Chapman and Hall, London, England. 205 pp.
 2000 Global patterns in biodiversity. *Nature* 405:220-227.
 2003 *The Structure and Dynamics of Geographic Ranges.* Oxford University Press, Oxford, England. 266 pp.
- Gaston, K. J., T. M. Blackburn, and J. H. Lawton
 1997 Interspecific abundance-range size relationships: An appraisal of mechanisms. *Journal of Animal Ecology* 66:579-601.
- Gaston, K. J., and W. E. Kunin
 1997 Rare-common differences: An overview. Pp. 12-29 in *The Biology of Rarity: Causes and Consequences of Rare-Common Differences* (Kunin, W. E., and K. J. Gaston, eds.). Chapman and Hall, London, England.

Cofré et al.: Small Mammal Species Richness in Chile

- Gillespie, T. W.
2002 Latitudinal extent and natural history characteristics of birds in Nicaragua. *Global Ecology and Biogeography* 11:411-417.
- Graham, M. H.
2003 Confronting multicollinearity in ecological multiple regression. *Ecology* 84:2809-2815.
- Harcourt, A. H., S. A. Coppeto, and S. A. Parks
2002 Rarity, specialization and extinction in primates. *Journal of Biogeography*. 29:445-456.
- Harvey, P. H., and M. D. Pagel
1991 *The Comparative Method in Evolutionary Biology*. Oxford University Press, Oxford, England. 239 pp.
- Hawkins, B. A.
2004 Summer vegetation, deglaciation and the anomalous bird diversity gradient in eastern North America. *Global Ecology and Biogeography* 13:321-325.
- Hawkins, B. A., and E. E. Porter
2004 Relative influences of current and historical factors on mammal and bird diversity patterns in deglaciated North America. *Global Ecology and Biogeography* 12:475-481
- Hobbs, T. J.
1995 The use of NOAA-AVHRR NDVI data to assess herbage production in the arid rangelands of Central Australia. *International Journal of Remote Sensing* 16:1289-1302
- Hubbell, S. P.
2001 A unified null theory of biogeography and relative species abundance. *Monographs in Population Biology* 32. Princeton University Press, Princeton, New Jersey, USA. 375 pp.
- Hurlbert, A. H.
2004 Species-energy relationships and habitat complexity in bird communities. *Ecology Letters* 7:714-720.
- Hurlbert, A. H., and J. P. Haskell
2003 The effect of energy and seasonality on avian species richness and community composition. *American Naturalist* 161:83-97.
- Jaksic, F. M.
1997 *Ecología de los Vertebrados de Chile*. Ediciones Universidad Católica de Chile, Santiago, Chile. 262 pp.

- Jetz, W., and C. Rahbek
2002 Geographic range size and determinants of avian species richness. *Science* 297:1548-1551.
- Jiménez, J. E., P. Feisinger, and F. M. Jaksic
1992 Spatiotemporal patterns of an irruption and decline of small mammals in north-central Chile. *Journal of Mammalogy* 73:356-364.
- Jiménez, J. E., P. A. Marquet, R. Medel, and F. M. Jaksic
1991 Comparative ecology of Darwin's fox (*Pseudalopex fulvipes*) in mainland and island settings of southern Chile. *Revista Chilena de Historia Natural* 63:177-186.
- Johnson, W. E., W. L. Franklin, and J. A. Iriarte
1990 The mammalian fauna of the northern Chilean Patagonia: a biogeographical dilemma. *Mammalia* 54:547-469.
- Jones, C. B.
1997 Rarity in primates: implications for conservation. *Mastozoología Neotropical* 4:35-47.
- Kaspari, M., S. O'Donnell and J. R. Kercher
2000 Energy, density, and constraints to species richness: Ant assemblages along a productivity gradient. *American Naturalist* 155:280-293.
- Kelt, D. A.
1994 The natural history of small mammals from Aisén Region, southern Chile. *Revista Chilena de Historia Natural* 67:183-207.
- Kelt, D. A., M. Taper, and P. L. Meserve
1994 Assessing the impact of competition on community assembly: a case study using small mammals. *Ecology* 76:1283-1296.
- Kerr, J. T.
1997 Species richness, endemism, and the choice of areas for conservation. *Conservation Biology* 11:1094-1100
- Kerr, J. T., and L. Packer
1997 Habitat heterogeneity as a determinant of mammal species richness in high-energy regions. *Nature* 385:252-254
- Kunin, W. E., and K. J. Gaston
1993 The biology of rarity: Patterns, causes, consequences. *Trends in Ecology and Evolution* 8:298-301.
- Legendre, P., and L. Legendre,
1998 *Numerical Ecology*. 2nd ed. Elsevier, Amsterdam. 853 pp.

Cofré et al.: Small Mammal Species Richness in Chile

- Legendre, P., F. J. Lapointe, and P. Casgrain
1994 Modelling brain evolution from behaviour: a permutational regression approach. *Evolution* 48:1487-1499.
- Lemoine, N., and K. Böhning-Gaese
2003 Potential impact of global climate change on species richness of long-distance migrants. *Conservation Biology* 17:1-11.
- Lyons, S. K., and M. R. Willig
1999 A hemispheric assessment of scale dependence in latitudinal gradients of species richness. *Ecology* 80:2483-2491.
- Manly, B. F. J.
1986 Randomization and regression methods for testing for association with geographical, environmental, and biological distances between populations. *Researches on Population Ecology* 28:201-218.
- Mann, G. F.
1978 Los Pequeños Mamíferos de Chile: Marsupiales, Quirópteros, Edentados y Roedores. *Gayana (Zoología)* 40:1-342.
- Manne, L., and S. Pimm
2001 Beyond eight forms of rarity: Which species are threatened and which will be next? *Animal Conservation* 4:221-229.
- Manne, L. L., T. M. Brooks, and S. L. Pimm
1999 Relative risk of extinction of passerine birds on continents and islands. *Nature* 399:258-261.
- Mantel, N.
1967 The detection of disease clustering and a generalized regression approach. *Cancer Research* 27:209-220.
- Marquet, P. A., M. Fernández, S. A. Navarrete, and C. Valdovinos.
2004 Diversity emerging: towards a deconstruction of biodiversity patterns. Pp. 191-209 in *Frontiers of Biogeography: New directions in the Geography of Nature* (Lomolino, M., and L. R. Heaney, eds). Sinauer Associates, Sunderland, Massachusetts, USA.
- Medel, R. G., J. E. Jiménez, F. M., Jaksic, J. L. Yañez, and J. J. Armesto
1990 Discovery of a continental population of the rare Darwin's fox *Dusicyon fulvipes* (Martin, 1837) in Chile. *Biological Conservation* 51:71-77.
- Mercer, J. H.
1983 Cenozoic glaciations in the Southern hemisphere. *Annual Review of Earth and Planetary Science* 11:99-132.

- Meserve, P. L., and F. M. Jaksic
 1991 Comparaciones de ensambles de vertebrados terrestres en pluviselvas templadas de Norte y Sudamerica. *Revista Chilena de Historia Natural* 64:511-536.
- Meserve, P. L., D. A. Kelt, and D. R. Martínez
 1991 Geographical ecology of small mammals in continental Chile Chico, South America. *Journal of Biogeography* 18:179-187
- Mönkkönen, M., and P. Viro
 1997 Taxonomic diversity of the terrestrial bird and mammal fauna in temperate and boreal biomes of the northern hemisphere. *Journal of Biogeography* 24:603–612.
- Muñoz A., and J. Yañez
 2000 Mamíferos de Chile. CEA Ediciones, Valdivia, Chile. 464 pp.
- Murray, B. R., P. H. Thrall, A. M. Gill, and A. B. Nicotra
 2002 How plant life-history and ecological traits relate to species rarity and commonness at varying spatial scales. *Austral Ecology* 27:291-310.
- Murúa, R.
 1996 Comunidades de mamíferos del bosque templado de Chile. Pp. 113 – 134 in *Ecología de los Bosques Nativos de Chile* (Armesto, J. J., C. Villagrán, and M. K. Arroyo, eds.). Editoria Universitaria. Santiago, Chile.
- Nychka, D.
 2004 Fields: Tools for spatial data. R package version 2.0. Online at <http://www.cgd.ucar.edu/stats/Software/Fields>
- Oberrath, R., and K. Böhning-Gaese
 2001 Signed Mantel Test to cope with autocorrelation in comparative analyses. *Journal of Applied Statistics* 28:725-736.
- 2002 Phenological adaptation of ant-dispersed plants to seasonal variation in ant activity. *Ecology* 83:1412-1420.
- Palma, R. E., E. Rivera-Milla, J. Salazar-Bravo, F. Torres-Pérez, U. F. J. Pardiñas, P. A. Marquet, A. E. Spotorno, A. P. Meynard, and T. L. Yates
 2005 Phylogeography of *Oligoryzomys longicaudatus* (Rodentia: Sigmodontinae) in temperate South America. *Journal of Mammalogy* 86: 191-200.
- Paruelo, J. M., E. G. Jobbágy, and O. E. Sala
 2001 Current distribution of ecosystem functional types in temperate South America. *Ecosystems* 4:683-698.
- Paruelo, J. M., E. G. Jobbágy, O. E. Sala, W. K. Lauenroth, and I. C. Burke
 1998 Functional and structure convergence of temperate grassland and

shrubland ecosystems. *Ecological Applications* 8:194-206.

Pearson, O. P.

1983 Characteristics of a mammalian fauna from forest in Patagonia, southern Argentina. *Journal of Mammalogy* 64:476-492.

1984 Taxonomy and natural history of some fossorial rodents of Patagonia, southern Argentina. *Journal of Zoology* 202:225-237.

Pearson, O. P., and A. K. Pearson

1982 Ecology and biogeography of the southern rainforest of Argentina. Pp. 129-142 in *Mammalian Biology in South America* (Mares, M. A., and H. H. Genoways, eds.). Pymatuning Laboratory of Ecology, University of Pittsburgh, Special Publication Series 6. Pittsburgh, Pennsylvania, USA.

Pimm, S., H. Jones, and J. Diamond

1988 On risk of extinction. *American Naturalist* 132:757-785.

Prendergrast, J. R., R. M. Quinn, J. H. Lawton, B. C. Eversham, and D. W. Gibbons

1993 Rare species, the coincidence of diversity hotspots and conservation strategies. *Nature* 365:335-337.

Purvis, A., J. L. Gittleman, G. Cowlishaw, and G. M. Mace

2000 Predicting extinction risk in declining species. *Proceedings of the Royal Society of London B* 267:1947-1952

R Development Core Team

2005 R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Online at <http://www.R-project.org>.

Rabinowitz, D. S., S. Cains, and T. Dillon

1986 Seven forms of rarity and their frequency in the flora of the British Isles. Pp. 182-204 in *Conservation Biology: The Science of Scarcity and Diversity* (Soulé, M. E., ed.). Sinauer Associates, Sunderland, Massachusetts, USA.

Redford, K. H., and J. K. Eisenberg

1992 *Mammals of the Neotropics. Vol. 2: The Southern Cone of South America.* University of Chicago Press, Chicago, Illinois, USA. 430 pp.

Reise, D., and W. Venegas

1987 Catalogue of records, localities, and biotopes for research work on small mammals in Chile and Argentina. *Gayana (Zoologica)* 51:103-130.

- Ricklefs, R, and D. Schluter (eds.)
1993 Species Diversity in Ecological Communities: Historical and Geographical Perspectives. University of Chicago Press. Chicago, Illinois, USA. 414 pp.
- Rodríguez, P., and H. T. Arita
2004 Beta diversity and latitude in North American mammals: Testing the hypothesis of covariation. *Ecography* 27:547-556.
- Romdal, T. S., R. K. Colwell, and C. Rahbek
2005 The influence of band sum area, domain extent, and range sizes on the latitudinal mid-domain effect. *Ecology* 86:235-244.
- Rosenzweig, M. L.
1995 Species Diversity in Space and Time. Cambridge University Press, Cambridge. USA, 458 pp.
- Ruggiero, A. and T. Kitzberger
2004 Environmental correlates of mammal species richness in South America: effects of spatial structure, taxonomy and geographic range. *Ecography* 27:401-416.
- Saavedra B., and J. A. Simonetti
2000 A northern and threatened population of *Irenomys tarsalis* (Mammalia: Rodentia) from Central Chile. *Zeitschrift für Säugetierkunde* 65:243-245.
2001 New records of *Dromiciops gliroides* (Microbiotheria: Microbiotheriidae) and *Geoxus valdivianus* (Rodentia: Muridae) in central Chile: their implications for biogeography and conservation. *Mammalia* 65:96-100.
2003 Holocene distribution of Octodontid rodents in central Chile. *Revista Chilena de Historia Natural* 76: 383-389.
- Smith, M. F., D. A. Kelt, and J. L. Patton
2001 Testing models of diversification in mice in the *Abrothrix olivaceus/xanthorhinus* complex in Chile and Argentina. *Molecular Ecology* 10:397-405.
- Smouse, P. E., J. C. Long, and R. R. Sokal
1986 Multiple regression and correlation extensions of the Mantel test of matrix correspondence. *Systematic Zoology* 35:627-632.
- Spotorno, A. E., H. Cofré, G. Manríquez, Y. Vilina, P. A. Marquet, and L. I. Walker
1998 Una nueva especie de *Loxodontomys*, otro mamífero filotino en los Andes de Chile central. *Revista Chilena de Historia Natural* 71:359-373.

Cofré et al.: Small Mammal Species Richness in Chile

- Spotorno, A. E., L. I. Walker, S. V. Flores, M. Yevenes, J. C. Marín, and C. Zuleta
2001 Evolución de los filotinos (Rodentia, Muridae) en los Andes del Sur. *Revista Chilena de Historia Natural* 74:151-166.
- Taylor, C. M., and N. J. Gotelli
1994 The macroecology of *Cyprinella*: correlates of phylogeny, body size, and geographical range. *American Naturalist* 144:549-569
- Tognelli, M. F., and D. A. Kelt
2004 Analysis of determinants of mammalian species richness in South America using spatial autoregressive models. *Ecography* 27:427- 436.
- Van Rensburg, B. J., S. L. Chown, and K. J. Gaston
2002 Species richness, environmental correlates, and spatial scale: A test using South African birds. *American Naturalist* 159:566-577.
- Vázquez, L.-B., and K. J. Gaston
2004 Rarity, commonness, and patterns of species richness: The mammals of Mexico. *Global Ecology and Biogeography* 13:535-542.
- Villagrán, C.
1995 Quaternary history of the Mediterranean vegetation of Chile. Pp 3–20 in *Ecology and Biogeography of Mediterranean Ecosystems in Chile, California and Australia* (Arroyo, M. K., P. H. Zedler, and M. D. Fox, eds.). Springer Verlag, Berlin, Germany. 455 pp.
- Villagrán, C., P. Moreno, and R. Villa
1996 Antecedentes palinológicos acerca de la historia cuaternaria de los bosques chilenos. Pp 51–70 in *Ecología de los Bosques Nativos de Chile* (Armesto, J. J., C. Villagrán, and M. K. Arroyo, eds.). Editoria Universitaria, Santiago, Chile.
- Vuilleumier, B. S.
1971 Pleistocene changes in the fauna and flora of South America. *Science* 173:771–780.
- Whittaker, R. H., K. J. Willis, and R. Field
2001 Scale and species richness: towards a general, hierarchical theory of species diversity. *Journal of Biogeography* 28:453 - 470
- Williams, P., D. Gibbons, C. Margules, A. Rebelo, C. Humpries, and R. Pressley
1996 A comparison of richness hotspots, rarity hotspots, and complementary areas for conserving diversity of British birds. *Conservation Biology* 10:155-174.

Yañez, J., and A. Muñoz-Pedreroz

2000 Mamíferos vivientes de Chile. Mamíferos de Chile. Pp. 37-40 in Mamíferos de Chile (Muñoz-Pedreroz, A., and J. Yañez, eds.). Ediciones CEA, Valdivia, Chile.

Zar, J. H.

1999 Biostatistical Analysis. Fourth Edition, Prentice Hall, Upper Saddle River, New Jersey, USA. 929 pp.