

# Diversity and distribution of small mammals in the South American Dry Andes

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**Abstract** The Andean mountain range has played an important role in the evolution of South American biota. However, there is little understanding of the patterns of species diversity across latitudinal and altitudinal gradients. In this paper, we examine the diversity of small mammals along the South Central Dry Andes (SCDA) within the framework of two contrasting hypotheses: (a) species richness decreases with increasing elevation and latitude; and (b) species richness peaks at altitudinal midpoints (mid-domain). We explore the composition of the species pool, the impact of species–area relationships and the Rapoport effect (i.e. size of geographic ranges) along latitudinal and elevational gradients. First, we constructed a database of SCDA small mammals. Then, species richness patterns were analysed through generalized models, and species–area relationships were assessed by log–log regressions; the curvilinear method ( $c = S/Az$ ) was used to compute richness corrected by area size. Lastly, the Rapoport effect was evaluated using the midpoint method. Our results show: (1) a richness of 67 small mammals along the SCDA, of which 36 are endemic; (2) a hump-shaped pattern in species richness along elevation and latitudinal gradients; (3) a species–area relationship for both gradients; (4) endemic species corrected by area present a strong and positive relationship with elevation; (5) a Rapoport effect for the latitudinal ranges, but no effect across the elevational gradient; and (6) a major species turnover between 28° and 30° south latitude. This is the first study quantifying the diversity of small mammals encompassing the central Andean region. Overall, our macrogeographic analysis supports the previously postulated role of the Andes in the diversification of small mammals (i.e. *in situ* cladogenesis) and highlights some basic attributes (i.e. anatomy of geographic ranges; species–area relationships) when considering the consequences of climate change on biodiversity conservation of mountain ecosystems.

**Key words:** Andean ecoregion, distributional range, gradient, mountain, richness, species–area relationship.

## INTRODUCTION

The South American Andes extend over 8500 km (Orme 2007) and represent a good example of the role of mountains as biogeographic barriers for biodiversity (Young *et al.* 2007). The Andes uplift prompted the formation of new dry high-elevation habitats due to its blocking effect upon the moist winds from the Pacific (Young *et al.* 2007). These new habitats (i.e. Altiplano, Puna and Atacama Desert, among others) were suitable for local biota differentiation. Moreover, the Andean uplift led to species colonization, isolation events and singularity of biota on either side of the Andean mountain range (Marshall 1979; Ojeda *et al.* 2000; Palma *et al.* 2005; Brumfield & Edwards 2007).

The Andes served as a dispersal route for species reaching South America after the Great Biotic American Interchange (GABI; Marshall 1979). These geological events resulted in a diversity of topographies,

climates and habitats (i.e. history of place) which contributed to the high diversity and endemism (history of lineages) of mammals in this area (Herskovitz 1969; Reig 1981, 1986; Marquet 1994).

Global and regional scale patterns of diversity are often associated with elevation and latitudinal gradients (Terborgh 1977; Rahbek 1995, 1997; Rosenzweig 1995; Brown 2001; Lomolino 2001). Range size and position along the gradient reflects the influence of environmental conditions on species survival and reproduction. These environmental conditions vary across latitudes and altitudes throughout the world (Rahbek 1995; Rosenzweig 1995; Brown 2001; Lomolino 2001). However, species with small geographic ranges (endemics) tend to show a pattern in richness different to that of other, more widespread species (Jetz *et al.* 2004). For example, endemics are affected by different conditions than wide-range species (i.e. topographic heterogeneity is considered the most important predictor of narrow-ranging species, meanwhile productivity is the main driver of wide-range species distribution) (Stotz 1998; Jetz & Rahbek 2002).

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Two general hypotheses have been proposed for how species richness is related to altitude or latitude: either species richness decreases with increasing elevation or latitude (Simpson 1964; Stevens 1992), or species richness peaks at midpoints (Rahbek 1995; Heaney 2001; Rickart 2001; Sanchez-Cordero 2001; McCain 2005). Some of the proposed processes accounting for richness patterns along gradients are species–area relationships (Rosenzweig 1995), species–energy relationship (Wright 1983) and mid-domain effect (Colwell & Hurtt 1994).

Previous studies regarding small mammal diversity at smaller scales along the Andes, such as the Puna and Atacama Desert, have found a positive relationship between elevation, area and species richness (Pearson & Pearson-Ralph 1978; Marquet 1994). However, in spite of the importance of the Andes in the evolution of South American biota (Marshall & Sempere 1993) and its use as a model for long-term climate change assessments (Bush 2002; Urrutia & Vuille 2009), there are no studies addressing the general patterns of diversity of small mammals along the Dry Andes.

The aim of our study was to characterize and quantify major diversity patterns of small mammal assemblages occurring in the South Central Dry Andes (henceforth SCDA). In particular, we addressed: (1) patterns of diversity and faunal similarity across latitudinal and elevational gradients; (2) species–area relationships; and (3) distribution of range sizes within latitudinal and elevational domains. We also analysed these same patterns for endemic species.

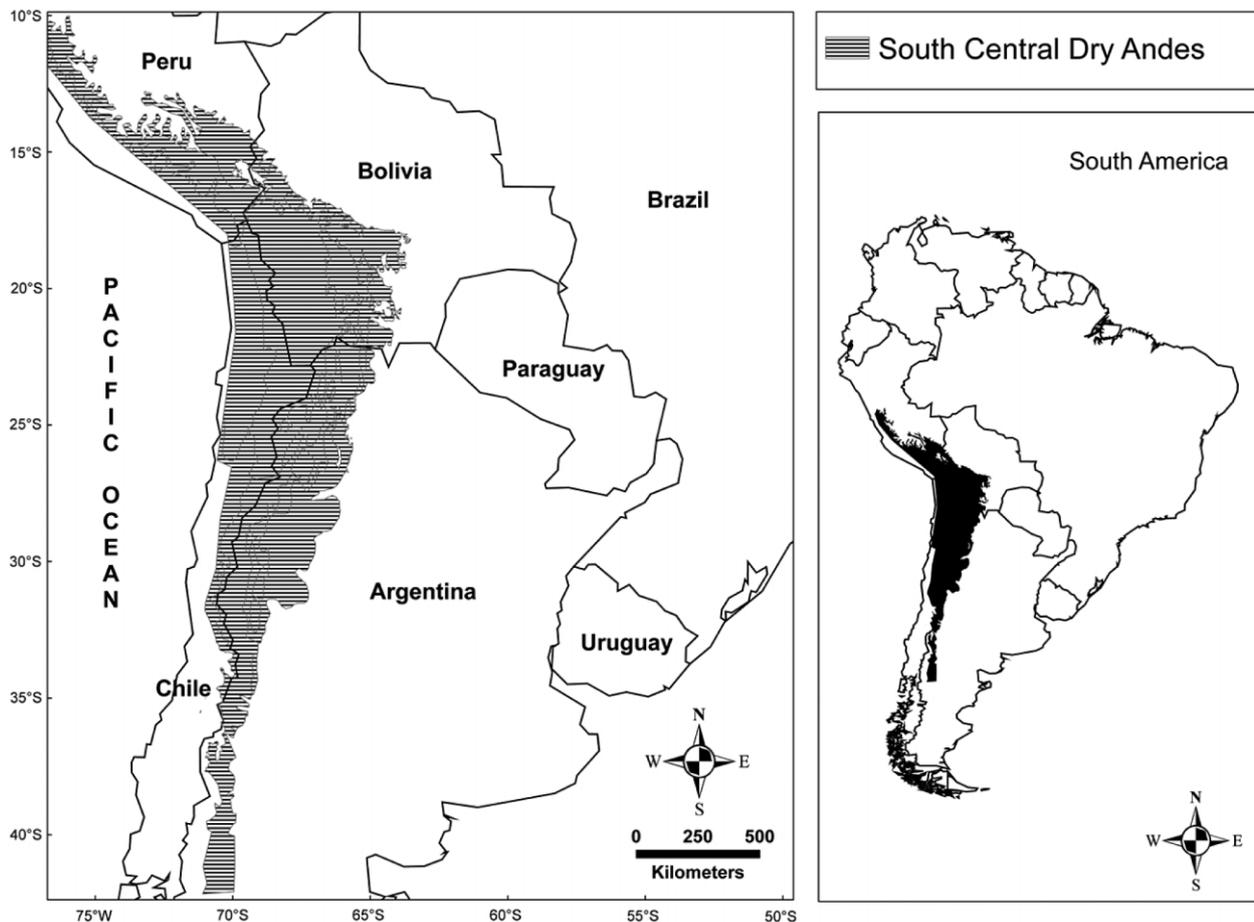
## DATA AND METHODS

### Study area

The SCDA region was defined between 8° and 42°S (Young *et al.* 2007; Sempere *et al.* 2008), which covers an altitudinal range from 800 to 6000 m a.s.l. (Fig. 1).

### Species composition

We generated a database of the occurrence of small mammals along the South American Dry Andes. The compilation of



**Fig. 1.** Map of the geographic location of South Central Dry Andes.

species accounting for each distributional range was based on Nature Serve database (Patterson *et al.* 2007) and adjusted and updated through an exhaustive review of scientific literature (Pearson 1982; Redford & Eisenberg 1992; Diaz & Barquez 2002; Wilson & Reeder 2005; see Appendix S1). We analysed the small mammal species patterns for two categories: total pool of species and those species restricted or endemic to the SCDA. We created a dissimilarity matrix of species, based on combined latitudinal and elevation midpoints. We used that information to construct dendrograms that would group species according to their geographical distribution.

### Latitudinal & altitudinal diversity patterns

We divided the latitudinal extension of the region into 2-degree bands and the elevational gradient into 200-m bands (Hurlbert & Jetz 2007). Several band sizes were analysed to evaluate how sensitive richness patterns are to the extent of geographic replicates (Appendix S2). A species was defined as present between its highest and lowest reported elevations (range interpolation) (Rahbek 1997; McCain 2009). Species richness along both gradients was quantified through the total number of species present at each band. We documented latitudinal and elevational species richness patterns using generalized linear models. Each generalized linear model was compared using Akaike's information criterion (AIC).

### Species–area relationships

The area hypothesis proposes that regions with largest area will have more species than smaller ones (Rosenzweig 1992, 1995). Along elevational gradients, area influences richness patterns in diverse manners (McCain 2007). Latitudinal and altitudinal band area was calculated using a zonal geometry tool performed by ArcGis 9.1 software. To evaluate the effect of area along the SCDA, we performed log–log linear regressions between richness and area size (latitudinal and altitudinal). We calculated richness values corrected by area size using the curvilinear method ( $c = S/Az$ ;  $c$  = area-corrected diversity estimate;  $S$  = species richness;  $A$  = area size, and  $z$  = value, which determines how rapidly diversity increases with increasing area) (Rosenzweig 1995; Rahbek 1997). We used a taxon-specific  $z$ -value ( $z = 0.22$ ) calculated by McCain (2007). This  $z$ -value was intended for non-volant small mammals (e.g. rodents, insectivores and marsupial mice) of several gradients (McCain 2007).

### Range size distribution

Relationships between range size and geographic gradients (latitude and elevation) were evaluated using the midpoint method (Rohde *et al.* 1993), which displays the latitudinal range of each species in relation to its latitudinal midpoint (Colwell & Hurr 1994). The midpoint method is preferable to the method proposed by Stevens (1989) because each data point is statistically independent (Rohde *et al.* 1993; Gaston

*et al.* 1998; Ruggiero & Werenkraut 2007). All statistical analyses were performed with R software version 2.9.0.

## RESULTS

### Species composition

We recorded 67 small mammal species (non-volant), belonging to eight families and 26 genera (see Appendix S1). Thirty-six of the 67 species are endemic to the SCDA. We distinguished three groups along the latitudinal gradient: a northern group (ranging from 8°S to 30°S), a group with ranges spanning the mid-latitudes and a southern group (from 30°S to 55°S) (Fig. 2a). No clear cut groups were found along the elevational gradient (Fig. 2b).

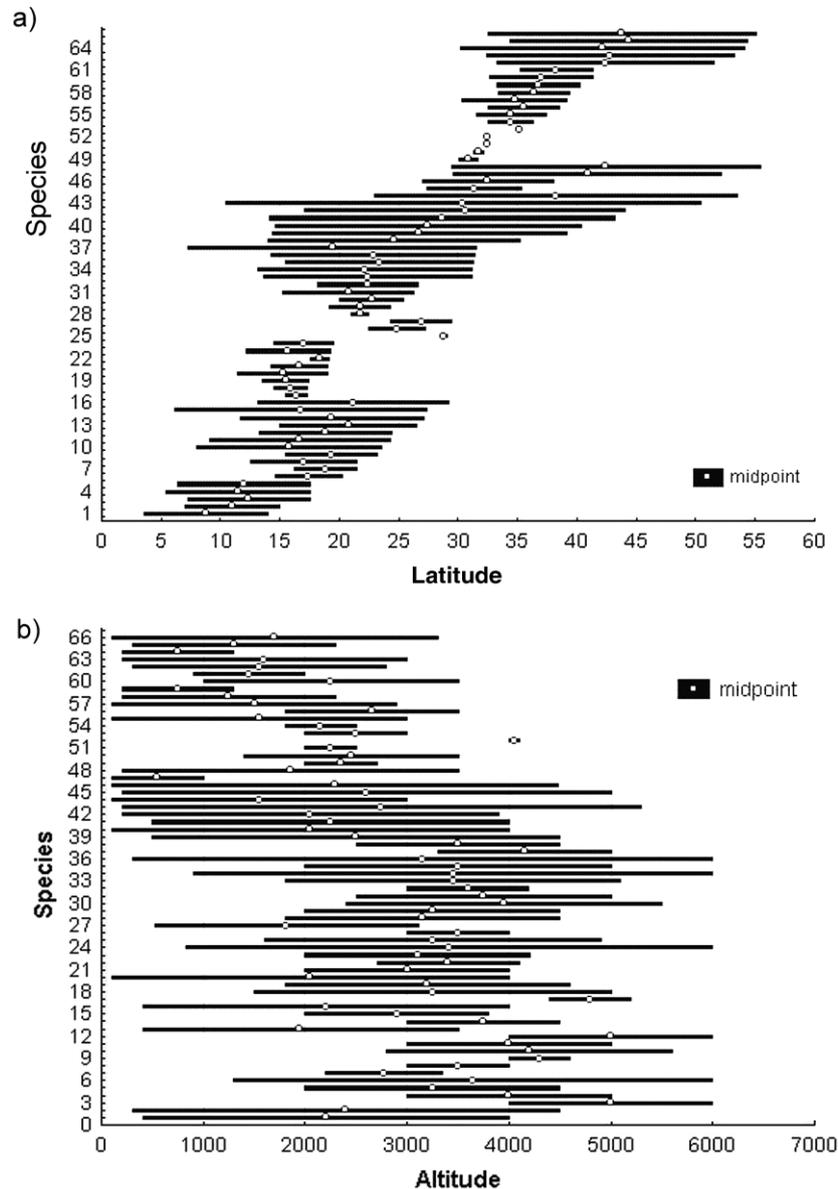
When both geographical dimensions (latitudinal and altitudinal) were analysed, four species groups were found (Fig. 3). Groups A and B (Fig. 3) were mainly northern species (11–32°S; 12–18°S respectively) being separated from each other by their altitudinal range. Group A had species with ranges spanning the mid-altitudes (2900–4300 m a.s.l.), while group B was restricted to high altitudes (4800–5000 m a.s.l.). Group C was composed of southern species (36–42°S) whose altitudinal span was narrow and confined to lowlands (i.e. 500–750 m a.s.l.), whereas group D represented broad range species (i.e. 8–44°S; 1200–2700 m a.s.l.).

### Latitudinal & altitudinal diversity patterns

The latitudinal and elevation gradient of total and endemic species richness portrayed a hump-shaped pattern (Fig. 4). Third- and second-order polynomials showed significant fit to latitudinal and elevation gradients, respectively. Both were considered the best-fit model (lowest AIC) (Table 1). The latitudinal richness peak for total species was located at 18°S with 34 species. A second peak of 25 species occurred at 36°S (Fig. 4a). The same bimodal pattern was found for endemic species, showing fewer species at high latitudes.

The elevational pattern for total and endemic species showed a richness peak between 3000 and 3500 m (50 and 30 species, respectively). Total species presented a non-symmetrical hump shape, with species richness decreasing at high elevations. On the other hand, endemic species presented a symmetrical shape with a decrease in species richness towards both ends of the gradient (Fig. 4b).

Once we analysed both geographic dimensions (latitude and altitude) as predictors for richness, this model accounted for 51% of the deviance explained for total species, and 71% for the endemics.



**Fig. 2.** (a) Latitudinal and (b) altitudinal ranges of species recorded along the South Central Dry Andes domain (see Appendix S3 for detailed species names).

### Species–area relationships

Area size varied along both gradients. At 30°S, there was a sharp decrease in area size, which coincided with a decline in species richness for both species data sets (e.g. total species and endemics; Fig. 5a). Area size for latitudinal bands accounted for 25% of richness variation for total species ( $R^2 = 0.25$ ,  $P = 0.04$ ) and 70% for endemic species ( $R^2 = 0.70$ ,  $P < 0.001$ ) (Fig. 5b). When species richness was corrected by area (c), third-order polynomials were considered the best-fit model (lowest AIC) to latitudinal and elevation gradients,

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respectively (Table 2). Species richness corrected by area size showed a positive relationship with latitude ( $R^2 = 0.35$ ,  $P = 0.014$ ) for total species and no significant trend for endemic species ( $R^2 = 0.06$ ,  $P = 0.3$ ) (Fig. 5c).

Area size presented its highest values at mid-elevations (3000–4500 m). This peak was in accordance with species richness which peaked approximately at the same elevation (Fig. 5d). Richness–altitudinal area relationship accounted for 90% of the altitudinal gradient variation for total species assemblage ( $R^2 = 0.91$ ,  $P < 0.001$ ) and 20% for

the endemic set ( $R^2 = 0.20$ ,  $P = 0.01$ ) (Fig. 5e). When species richness was adjusted by area size, there was no significant relationship along the altitudinal gradient for the total species group ( $R^2 = 0.06$ ,  $P = 0.18$ ). On the other hand, the endemic species exhibited a positive and significant relationship, which accounted for 57% of richness variation with altitude ( $R^2 = 0.57$ ,  $P < 0.001$ ) (Fig. 5f). Third-order polynomials were considered the best models to explain latitudinal and elevation gradients (Table 2).

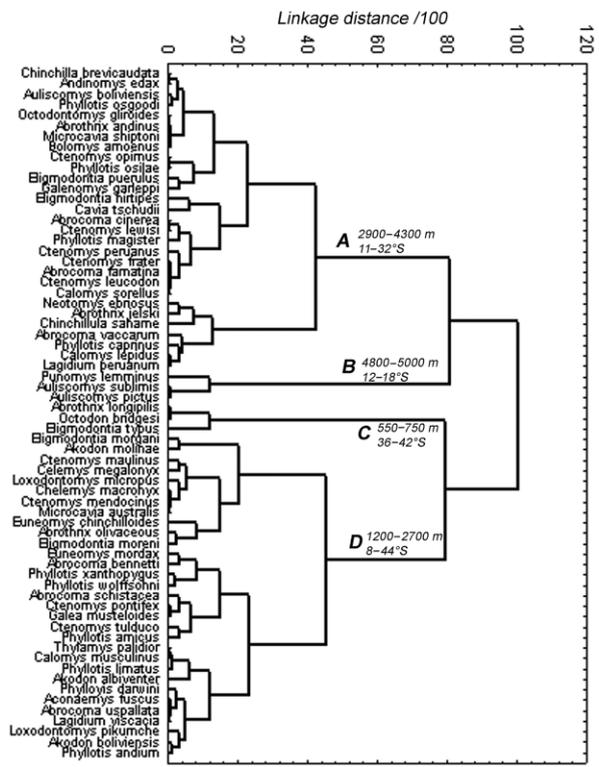
**Range size distribution**

Geographic ranges exhibited a positive trend with latitude for total species ( $R^2 = 0.06$ ,  $P = 0.03$ ); however, a similar trend was not registered for the endemic species ( $R^2 = 0.007$ ,  $P = 0.1$ ). Neither data set exhibited a Rapoport effect along the elevational gradient ( $R^2 = 0.0028$ ,  $P = 0.66$ ;  $R^2 = 0.0025$ ,  $P = 0.7$ ) (Fig. 6c,d).

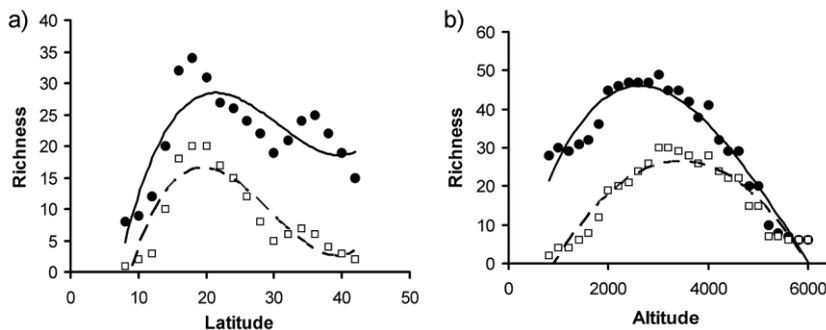
**DISCUSSION**

More than 50% of the small mammal species occurring in the SCDA are endemic. This supports earlier observations regarding the role of the South American highland desert ecosystem in the cladogenetic process of small mammals (Reig 1981; Pearson 1982; Marquet 1994). These high levels of endemism are attributed to the elevated speciation rates promoted by a particular set of environmental conditions, such as complex topography, narrow homothermal elevation zones and disjunct habitat distribution (Rahbek & Graves 2000).

Latitudinal and elevational richness gradient for both groups (total and endemic species) of Andean small mammals revealed similar patterns. The bimodal richness pattern found along the latitudinal extent of the Dry Andes, with its major and smaller peaks (18°S; 34–35°S), suggests that species turnover and decreasing species richness in the vicinity of 30°S represent a point of biogeographic divergence among two major biomes. This divergent point hypothesis is supported by faunal similarity analysis which differentiates these latitudinal assemblages. The northern assemblage corresponds to the Altiplano–Puna biome, mainly represented by species of high- and mid-altitudinal range, whereas the southern assemblage belongs to the Patagonia biome, represented by low-altitudinal species (Fig. 3). We suggest that the potential causes of this Andean gap are a reduction of suitable habitat, coupled with a gradual decline of the Andes elevation in the southern portion of the SCDA.



**Fig. 3.** Dendrogram of small mammal communities' similarities along latitudinal and altitudinal distributions simultaneously. Based on combined latitudinal and elevation geographic midpoints.

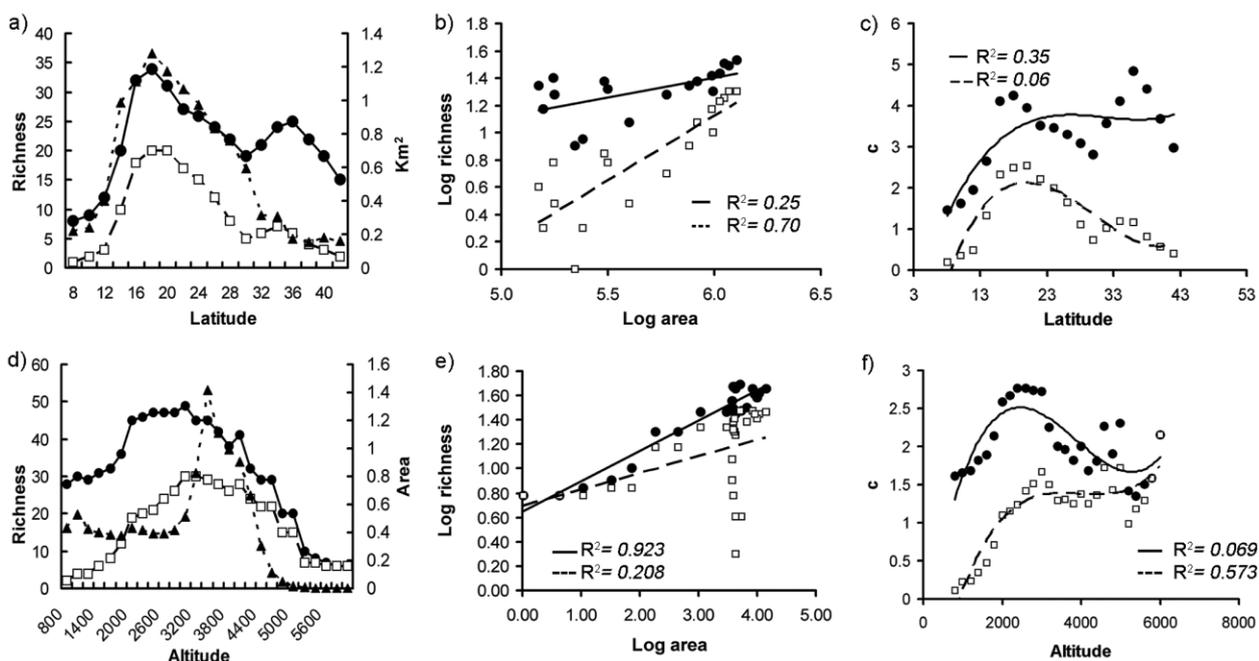


**Fig. 4.** (a) Latitudinal variation pattern in species richness. (b) Elevational variation pattern in species richness. Circle, total species; squares, endemic species.

**Table 1.** Richness–latitude and –altitude relationship, for total and endemic species

	Model	Deviance (%)		AIC		dAIC		Weight	
		Ts	Es	Ts	Es	Ts	Es	Ts	Es
Latitudinal pattern	Linear model	2.37	12.14	136.31	122	29.1	45.8	45.8	<0.001
	Quadratic model	53.68	21.06	114.7	89	7.5	13.6	13.6	0.001
	Cubic model	<b>74.25</b>	<b>27.95</b>	<b>107.23</b>	<b>76.2</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0.9</b>
Altitudinal pattern	Linear model	32.87	32.87	278.5	278.5	125.9	67.6	67.6	<0.001
	Quadratic model	95.43	51.68	153.59	240.4	0.9	29.4	29.4	<0.001
	Cubic model	<b>96.87</b>	<b>66.17</b>	<b>152.67</b>	<b>211</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>1</b>

Comparisons between linear, quadratic and cubic models. Boldface indicates best models. AIC, Akaike information criterion, dAIC, delta AIC; deviance (%), percentage of deviance explained by the model; Es, endemic species; Ts, total species; weight, Akaike weights.



**Fig. 5.** Species richness and area relationship along the latitudinal and altitudinal gradient of the South Central Dry Andes (circle, total species; squares, endemic species; triangle, area size). (a) Richness and area distribution along the latitudinal gradient. (b) Log–log species richness–latitudinal area relationship. (c) Species richness corrected by area size and latitude relationship. (d) Richness and area distribution along the altitudinal gradient. (e) Log–log species richness–altitudinal area relationship. (f) Species richness corrected by area size and altitude relationship.

A hump-shaped richness pattern along the elevation domain of SCDA corroborates previous results involving several taxa along different altitudinal gradients (Rahbek 1995). Moreover, hump-shaped richness patterns are commonly found among small mammals (Rahbek 1995; Heaney 2001; McCain 2005).

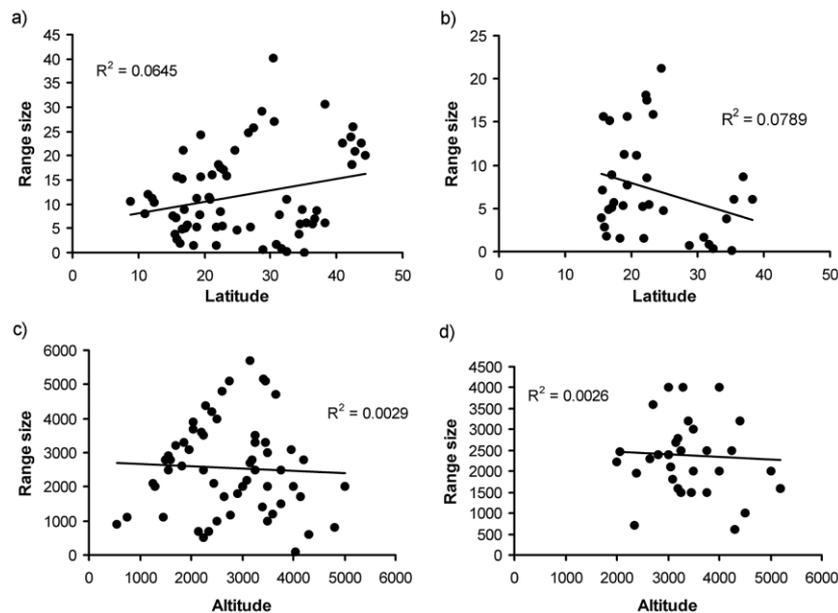
The latitudinal pattern of species richness for both groups suggests that area is an important factor regulating species richness across the SCDA. This pattern is consistent with previous observations for the small mammals of the Puna biome (Marquet 1994) and from North American intermountain region (Rickart 2001).

The strong positive correlation between endemic species richness and elevation in the SCDA contradicts the general pattern of decreasing richness with increased elevation (Stevens 1992; Rosenzweig 1995; Gaston & Blackburn 2000), and upholds the role of the Andes in the cladogenetic process of South American small mammals. Also, it is in accordance with the pattern found at a smaller scale for the Puna biome (Marquet 1994). Thus, a negative correlation between altitude and richness would be likely to arise if most speciation events had taken place in lowland habitats (Marquet 1994).

**Table 2.** Richness corrected by area size (c) relationship with latitude and altitude

	Model	AIC		dAIC		Weight	
		c-Ts	c-Es	c-Ts	c-Es	c-Ts	c-Es
Latitudinal pattern	Linear model	46.8	46.4	4.1	22.5	0.06	<0.001
	Quadratic model	43.1	33.6	0.4	9.7	0.41	0.007
	Cubic model	<b>42.7</b>	<b>23.9</b>	<b>0</b>	<b>0</b>	<b>0.51</b>	<b>0.99</b>
Altitudinal pattern	Linear model	35.3	22.4	19.2	18.6	<0.001	<0.001
	Quadratic model	27.7	12.5	11.6	8.8	0.003	0.01
	Cubic model	<b>16.1</b>	<b>3.7</b>	<b>0</b>	<b>0</b>	<b>0.99</b>	<b>0.98</b>

Comparisons between linear, quadratic and cubic models. Boldface indicates best models. AIC, Akaike information criterion; c-Es, endemic species; c-Ts, total species; dAIC, delta AIC; deviance (%), percentage of deviance explained by the model; weight, Akaike weights.



**Fig. 6.** Rapoport effect (Rohde *et al.* 1993) applied for latitudinal and altitudinal gradients. (a,c) Total species; (b,d) endemic species.

Species geographic ranges showed a positive Rapoport effect along the latitudinal gradient, with larger average range size occurring at higher latitudes. Explanations for Rapoport's rule are based on the hypothesis that climatic tolerances of temperate region species should be broad for them to be able to tolerate more variable climates (Janzen 1967; Stevens 1989; Ruggiero 1994; Gaston & Chown 1999). This positive Rapoport effect is not shown by endemic species and for neither assemblage at the altitudinal gradient. We hypothesize that the strong species–area relationship registered for these gradients seems to be the main factor regulating species distributional patterns. Area is one of several alternative explanations (i.e. climatic variables, productivity, ecoregion size, speciation–extinction dynamics or competition, among others)

which have been mentioned as predictors of these patterns (Colwell & Hurtt 1994; Gaston *et al.* 1998).

In accordance with previous studies, most species show intermediate or small distributional ranges along the altitudinal gradient (Ruggiero 1994; Ruggiero *et al.* 1998; Hawkins & Felizola Diniz-Filho 2006). The prevalence of small and intermediate ranges is an important factor in the light of climate change scenario (Pearson & Dawson 2003; Moritz *et al.* 2008).

### Climate change and regional implications

The climate change scenario has driven scientific interest in mountain ecosystems in relation to shifts in species geographic ranges along environmental gradi-

ents, particularly as a threat to endemic species with narrow geographic ranges (Pearson & Dawson 2003; Moritz *et al.* 2008).

Climate change (i.e. temperature increase) is expected to force species inhabiting mountain ecosystems to shift towards higher elevations (Parmesan 2006; Kerr & Kharouba 2007; Moritz *et al.* 2008). Moritz *et al.* (2008) found that for most small mammals inhabiting Yosemite National Park, distributional ranges shifted upward, which occurred more frequently for lower than upper limits. Moreover, lowland and highland species tended to expand and contract their ranges, respectively. However, predicting changes in the assemblage of small mammals will be difficult. Species responses are likely to be individualistic (i.e. linked to autoecological characteristics), depending on their body size, metabolic strategies, rates of metabolic variation, dispersal ability, life history specialization, availability of resources, landscape connectivity, and so on (O'Grady *et al.* 2004; Kerr & Kharouba 2007 and references therein). Furthermore, climate change scenarios predict temperature increases associated with variation in precipitation and seasonality (Thuiller 2007), which can alter the climatic conditions of mountainous areas creating new, more humid and warmer habitats, which can then be colonized by lowland species. In other words, this would reduce the area of 'dry and cold habitats', contracting and expanding the low and higher limits of species ranges, respectively. Briefly, changes in climatic conditions are likely to cause widespread alteration in the geographic ranges and abundances of species, resulting in changes in patterns of diversity (Hawkins *et al.* 2003).

In conclusion, the reported patterns of small mammal diversity across the Dry Andes highlight: (a) the concepts of site and lineage histories, supporting the role of the Andean mountain range in the diversification of Neotropical biota (i.e. high endemism); (b) the strong species–area relationships along both gradients; (c) high richness of endemic species positively associated with elevation; and (d) the relevance of understanding the macroscopic structure of geographic ranges as important baseline data for biodiversity conservation in mountain ecosystems.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** List of small non-volant mammals from the South Central Dry Andes.

**Appendix S2.** Richness latitudinal and altitudinal gradients.

**Appendix S3.** Species names referred to in Figure 2.