

Latitudinal and altitudinal patterns of the endemic cacti from the Atacama desert to Mediterranean Chile

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ABSTRACT

In this study we describe the biogeographic patterns of the endemic cacti from the Atacama Desert to the Mediterranean area of Chile. Our goals were: (1) to identify areas of high endemism, (2) to test Rapoport's rule, (3) to test the geometric constraints hypothesis, (4) to explore temperature and precipitation as explanatory variables of species richness. We used a list of 72 species of cacti, ranging from 18° to 36° S and from 0 to 4500 m.a.s.l. A Bayesian analysis of Endemicity (BAE) was used to evaluate hierarchical relationships of endemism between different latitudinal bands. Rapoport's rule was evaluated by examining the relationships between latitudinal/altitudinal mid-point, latitudinal/altitudinal range extent and species richness. The geometric constraints hypothesis was tested by examining the existence of mid-domain effect. The BAE indicated two areas of endemism: (1) the northern area between 18° S and 26° S, and (2) the southern area between 27° S and 36° S. The shape of the latitudinal gradient is non-linear, supporting the geometric constraints hypothesis. Altitudinal patterns, however, support Rapoport's rule; a peak of endemism was found at low altitudes. The explanatory variables were elevation, minimum temperature of the coldest month, mean temperature of wettest quarter and annual precipitation.

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1. Introduction

The increase in species richness from the poles to tropical areas is one of the oldest and broadest patterns documented in ecology (Brown and Lomolino, 1998; Willig et al., 2003). Furthermore, the decline in species richness with altitude and a humped pattern with a richness peak at intermediate elevations are also widely accepted (Colwell et al., 2009; McCain, 2004; Rahbek, 1995; Stevens, 1992). However, neither latitude nor altitude by itself is a direct driver of species richness, as these differences are related to latitudinal or altitudinal covariates (e.g. precipitation, temperature, area). Indeed, strong statistical support of contemporary climate control of large-scale biogeographic patterns is a widespread and accepted conviction (Hawkins et al., 2003).

Rapoport's rule and geometric constraints are major hypotheses that have been invoked as causes for latitudinal and altitudinal gradients. Rapoport's rule predicts that environmental

gradients can produce selective pressures, resulting in decreased species richness and increased distribution range towards the poles and mountain peaks because only organisms with broad climatic tolerances will be favoured by natural selection in these areas (Rapoport, 1979; Stevens, 1989, 1992; Willig et al., 2003). Latitudinal evaluations have demonstrated that Rapoport's rule is not always satisfied in the Southern Hemisphere (Mourelle and Ezcurra, 1997a). However Rapoport's rule indeed applied to bathymetric patterns of southern polychaetes (Moreno et al., 2008) and to elevation gradients in vertebrates (McCain, 2009). Whether the rule applies to elevation gradients in southern plant groups is unknown. Geometric constraints of geography are also known to affect biodiversity patterns, resulting in the mid-domain effect, in which the random placement of species' ranges within a hard-bounded geographic domain generates a peak of species richness near the centre of the altitudinal or latitudinal domain (Colwell and Hurtt, 1994; Grytnes and Vetaas, 2002). These two hypotheses produce different predictions of the shape of species richness curves: Rapoport's rule predicts a monotonic decrease along the altitudinal and latitudinal domain, while the geometric constraints hypothesis predicts a hump-shaped pattern.

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However, Rapoport's rule and geometric constraints can operate simultaneously, because of the complex interaction with other explanatory variables, thus varying their explaining power between latitudinal, altitudinal or bathymetric species richness patterns (Currie and Kerr, 2008; Colwell et al., 2009).

The Atacama Desert and Mediterranean Chile are distinctive biogeographical provinces (Cowling et al., 1996; Rundel et al., 1991); they offer unique opportunities to test biogeographic hypotheses of species richness gradients, because they occur within the South American Arid Diagonal and the Andes Range, two major geological and climatic formations that produce both environmental gradients and hard geographic boundaries. Furthermore, the western slope of the Andes Range in Chile is longitudinally oriented and narrow, reducing possible geographic area effects. The Arid Diagonal is a belt that crosses South America diagonally from the northwest to the south-eastern slopes of the Andes Range (Houston, 2006), producing environmental gradients that affect precipitation regimes, primary production and seasonality, which increase with latitude (Arroyo et al., 1988; Luebert and Pliscoff, 2006). This gradient can be easily observed in the change of arid vegetation zones from the northern deserts to the rainy temperate forests in southern Chile. Additionally, the Andes Range produces elevation gradients that lead to extreme climatic conditions characterised by a decrease in temperature, an increase in solar radiation and winds and shorter growing seasons (Stevens, 1992). Alternatively, the Arid Diagonal in the north, the Andes range in the east and the southern temperate forests of Chile may act as hard geographic boundaries to arid and tropical latitudinal species distributions. Finally, two other geographic constraints may be relevant, i.e. the coastline and the crest of the Andes; these may act as hard barriers affecting species richness patterns.

The relation of species richness gradients and endemic richness are critical to our understanding of the diversification of specious groups (such as Cactaceae). Species richness and endemism are expected to be coupled when they are shaped by the same isolation mechanisms (Vetaas and Grytnes, 2002). The endemism and species richness of Chilean cacti are one of the highest in the Chilean angiosperm families (Hoffmann and Walter, 2004; Hunt et al., 2006; Marticorena, 1990). All endemic cacti are exclusively distributed between 18° S and 36° S within the Chilean portion of the Arid Diagonal, suggesting that environmental gradients and hard geographic boundaries affect endemism patterns.

Quantitative biogeographical patterns for endemic Chilean cacti have not been studied in depth, in contrast to other countries such as Argentina and Mexico (Goettsch and Hernández, 2006; Hernández and Bárcenas, 1995, 1996; Mourelle and Ezcurra, 1996, 1997a,b). This consequently challenges our understanding of the speciation processes linked to the Arid Diagonal formation, achieving accurate predictions for the plant species of arid zones, consequences of global climate change and the creation of effective conservation initiatives (Hernández and Bárcenas, 1996). Lessons from Argentinean biogeographic patterns showed that Cactaceae richness is linked to favourable temperature and precipitation conditions (Mourelle and Ezcurra, 1996) and Rapoport's rule does not hold for latitudinal patterns in Argentinean cacti (Mourelle and Ezcurra, 1997a).

In this study we describe the biogeographical patterns of the endemic Chilean cacti, evaluating the role of the geometric constraints and Rapoport's rule hypotheses. Also we evaluated the role of climatic variables in determining latitudinal and altitudinal patterns of richness. In particular, our goals were (1) to identify areas of high endemism; (2) to test Rapoport's rule; (3) to test the geometric constraints hypothesis; and (4) to explore temperature and precipitation as explanatory variables of species richness.

2. Material and methods

2.1. Taxonomic database

The database used in this study consists of a list of 72 of endemic Chilean species of Cactaceae (see [Electronic Supplementary Material 1,2](#)). All the information is based on herbarium collections (CONC, SGO) and an exhaustive literature inspection. Although data obtained from herbarium collections and specific literature may be influenced by sampling effects, this potential problem is limited because the species of cacti have very narrow distribution ranges, reducing the possibility of unknown distribution limits. We also complemented literature and herbarium data with extensive field explorations. The literature employed in the analyses and amount of data per species can be accessed in [Electronic supplementary material 3 and 4](#), respectively.

2.2. Bayesian analysis of endemism (BAE)

We performed an analysis of endemism *via* the Markov Chain Monte Carlo method within a Bayesian framework (hereafter BMCMC). This procedure is similar to the Parsimony analysis of endemism (PAE, Morrone, 1994). Both BAE and PAE are analogous to phylogenetic hypothesis reconstruction; these approaches classify areas (analogous to taxa) by their shared endemic taxa (analogous to characters). BAE and PAE data consist of area × species matrices, and the resulting phylograms represent nested sets of areas in which the terminal branches of the area phylograms represent a single band of endemism (Morrone, 1994). The matrix for this study was prepared by coding taxa as absent (0) or present (1) in each 1° southern latitude band. Trees were rooted by a hypothetical area coded exclusively with zeros (called "latitude 17° S"), since species presence must be regarded as derived and species absence as primitive.

In the BMCMC, the Bayesian statistical procedure uses the empirical data (observations) to update a prior probability distribution to a posterior probability distribution (Ronquist, 2004). Posterior probability distributions are sampled by a Markov chain Monte Carlo method in order to obtain a stationary and most credible condition (see Ronquist, 2004 for details). Likelihood values and hypotheses of area relationships were generated using the M2P model with no reversible time (directional) implemented in the software BayesPhylogenies (Pagel and Meade, 2004). The M2P runs with presence/absence data with a non-time-reversible (i.e., directional) model, allowing the rates of change from 0 to 1 to differ from the rate of change from 1 to 0 (see BayesPhylogenies Manual, p. 5). In our study this corresponds to the number of species gained along lineages (i.e. branches of the tree) resulting from ecological processes of immigration and/or an evolutionary process of speciation. Approximately 9000 trees were generated using the BMCMC procedure, sampling every 1000th tree to assure that successive samples were independent. We graphically detected the convergence zone of the Markov Chain by plotting trees and their likelihood values, and then removing all trees sampled before the convergence zone (Pagel and Meade, 2004).

2.3. Latitudinal/altitudinal patterns of species richness and distribution ranges of species

We characterised the latitudinal patterns of species richness and distribution ranges of species based on a binary presence/absence matrix. The sum of elements along a row (i.e., latitudinal bands where the species is present) is the distributional range of a species, and the sum of elements along a column (i.e., number of species

within this latitudinal band) is the species richness in that latitudinal band. In this analysis, by species richness we mean the number of species occurring in a latitudinal band. Also, we characterised the altitudinal patterns of species richness and distribution ranges of species by constructing an altitudinal presence/absence matrix ranging from 0 to 4500 m.a.s.l. Again, rows represent species, but in this matrix columns are altitudinal bands of 250-m. Therefore, the sum of elements along a row is the distribution range of a species, and the sum of elements along a column is the species richness in that altitudinal band. By species richness we mean the number of species.

We contrasted the latitudinal/altitudinal patterns of species richness and distribution ranges of the Chilean endemic cacti with the predictions of: (1) Rapoport's rule, (2) geometric constraints. To test the Rapoport's rule model we analysed both species richness patterns and the distribution range of species, by examining their relationships with latitude/altitude, and their interactions. The Rapoport's rule hypothesis predicts a negative correlation between species richness and latitude/altitude, and a positive relationship of median distributional range for each species with latitude/altitude. Rapoport's rule was analysed using simple regression analyses and second-degree polynomial models implemented in R (ver. 2.6.2; <http://www.R-project.org>). To test the geometric constraints hypothesis we compared the observed pattern of species richness with the predicted curves constructed by a null model using the Monte Carlo simulation program Mid-Domain Null (McCain, 2004). Simulated curves were based on ranges of empirical sizes within a bounded domain, using the analytical stochastic models of Colwell and Hurtt (1994). We used 50,000 Monte Carlo simulations of empirical range size samples without replacement (i.e. the randomisation procedure) and with replacement (i.e. the bootstrap method) to calculate the amplitude of the 95% confidence simulation prediction curves (see Manly, 1997).

2.4. Climatic drivers of species richness

In addition to the evaluation of latitudinal/altitudinal patterns, we studied the underlying relationship between species richness and climatic variables utilising a latitude/longitude grid. In this analysis we wanted to reduce spatial autocorrelation to detect the influence of climate and elevation in determining variation in richness.

We selected some Bioclim variables from the WORLDCLIM dataset (Hijmans et al., 2005) by choosing one of a group of highly correlated variables. The employed variables were: annual mean temperature (Bio1), mean diurnal temperature range (mean of monthly [maximum temperature - minimum temperature]) (Bio2), isothermality (Bio3), minimum temperature of the coldest month (bio6), annual temperature range (Bio7), mean temperature of wettest quarter (Bio8), annual precipitation (Bio12), precipitation seasonality (Bio15) and precipitation of warmest quarter (Bio18). We computed simultaneous autoregressive (SAR) models to estimate regression coefficients while accounting for spatial autocorrelation of each of the climatic variables together with the interaction of annual mean temperature and annual precipitation (Rahbek et al., 2007; Rangel et al., 2010; Tognelli and Kelt, 2004). In this analysis, by species richness we mean the number of species occurring in a cell of the $0.5^\circ \times 0.5^\circ$ map, which approximates species density (Gotelli and Colwell, 2001; Rahbek et al., 2007).

3. Results

3.1. Bayesian analysis of endemism

The BAE showed two highly supported large areas of endemism: (1) the northern area between 18° S and 26° S, and (2) the southern area between 27° S and 36° S (Fig. 1). The longitude of the phylogram branches showed that within both areas endemism was

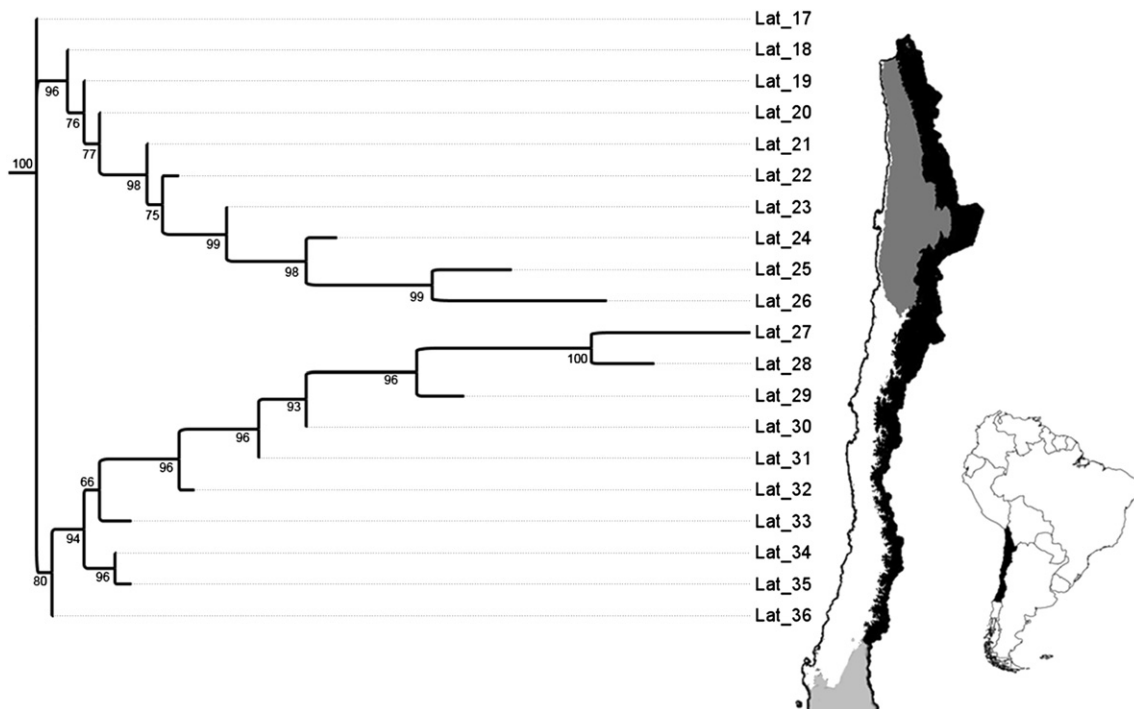


Fig. 1. Bayesian Analysis of Endemism of the distribution of the 72 endemic Chilean cacti in 1° latitude bands. Bayesian posterior probabilities $> 50\%$ are indicated behind branches. The black area within South America shows the studied area, the black area within Chile shows the Andes Range, the dark grey shows the hyper-arid desert, and the light grey shows the northern limit of temperate forests.

highest in north-central Chile and gradually decreased towards the extreme north and south (Fig. 1). The northern area showed the highest level of endemism between 23° S and 26° S, while the southern area showed the highest level of endemism between 27° S and 29° S (Fig. 1).

3.2. Latitudinal/altitudinal patterns of species richness

The latitudinal pattern of species richness showed a clear mid-domain effect (Fig. 2), in which the areas between 25° S and 28° S presented the highest species richness in the Chilean territory. A comparison of the empirical data with the 95% prediction curves of the simulation performed without and with replacement showed that 73.7% (14 of 19 points) and 57.9% (11 of 19 points), respectively, of the empirical richness points occurred within the predicted range of the analytical-stochastic null model (Fig. 2). Additionally, the simulation analysis indicated that at 21° S species richness is less than expected by the model.

The species richness curves of 250 m altitudinal bands did not provide empirical support for the mid-domain effect (Fig. 3). Moreover, the 95% prediction curves of the simulation without and with replacement showed that 5.6% (1 of 18 points) and 1.7% (3 of 18 points), respectively, of the empirical richness points occurred within the predicted range of the analytical-stochastic null model (Fig. 3).

Endemic Chilean cacti did not show a significant linear association between species richness and latitude ($r^2 < 0.001$, $F = 1.20$, $P = 0.274$). By contrast, a second-degree polynomial model showed a significant maximum latitudinal species richness at mid latitudes ($r^2 = 0.148$, $F = 28.90$, $P < 0.001$). Therefore, these analyses did not support the Rapoport's rule model in latitudinal species richness patterns.

The altitudinal patterns of species richness of the endemic Chilean cacti showed that species richness was negatively related with altitude ($r^2 = 0.362$, $F = 183.33$, $P < 0.001$). Similarly, a second-degree polynomial model showed a significant negative relationship between species richness and altitude, but with a greater portion of the variance explained by the model ($r^2 = 0.427$, $F = 120.95$, $P < 0.001$). Also we detected a significant relationship in the interaction between latitude and altitude in the linear model

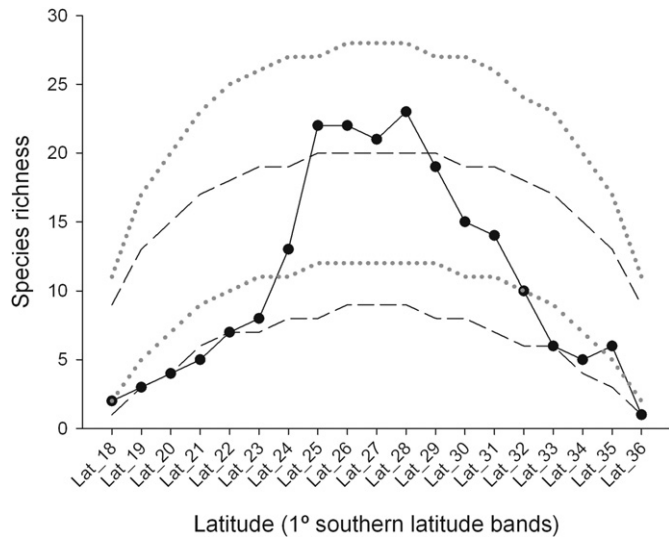


Fig. 2. Species richness found in each band of 1° latitude (black line with data points). The black dashed lines show the 95% prediction curves of sampling without replacement, and the dotted grey lines with replacement.

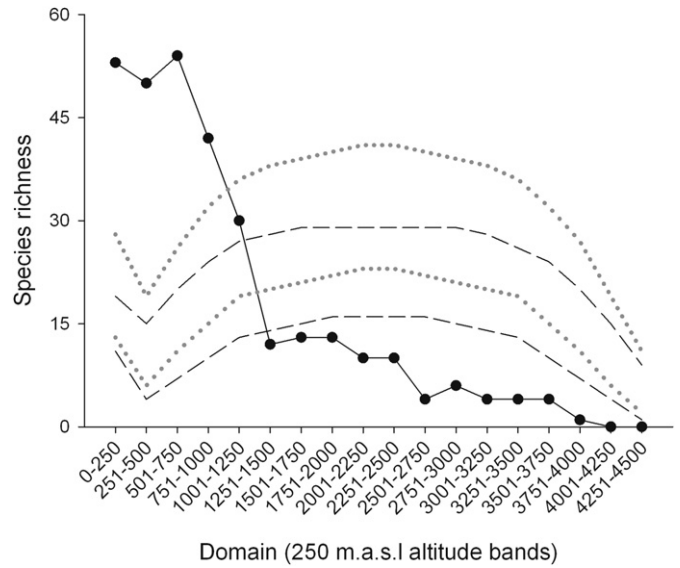


Fig. 3. Species richness found in each 250 m altitude band (black lines with data points). The black dashed lines show the 95% prediction curves of sampling without replacement, and the dotted grey lines with replacement.

($r^2 = 0.370$, $F = 4.42$, $P = 0.036$) and in the polynomial model ($r^2 = 0.362$, $F = 92.52$, $P < 0.001$), indicating that altitudinal patterns of species richness varied along latitudinal bands (Fig. 4).

3.3. Latitudinal/altitudinal patterns of distributional ranges of species

The median latitudinal range and latitude were not significantly related in endemic Chilean cacti ($r^2 = -0.014$, $F < 0.001$, $P = 0.987$) (Fig. 5). Moreover, the second-degree polynomial model was not significant ($r^2 = -0.025$, $F = 0.116$, $P = 0.890$). Also we did not detect a significant relationship between the median latitudinal range and altitude in the linear model ($r^2 = 0.03$, $F = 3.213$, $P = 0.08$) or in the polynomial model ($r^2 = 0.017$, $F = 1.632$, $P = 0.203$). A marginal relationship in the interaction between latitude and altitude in the

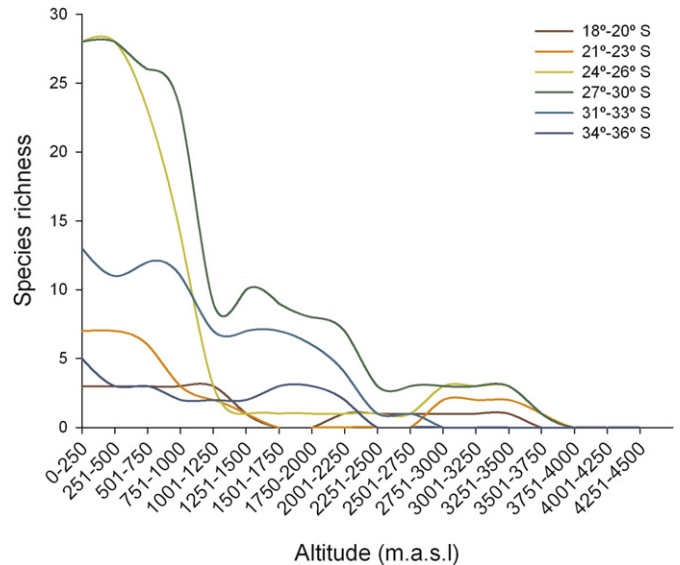


Fig. 4. Altitudinal gradient of species richness of endemic cacti at different latitudinal bands from 18° S to 36° S in Chile.

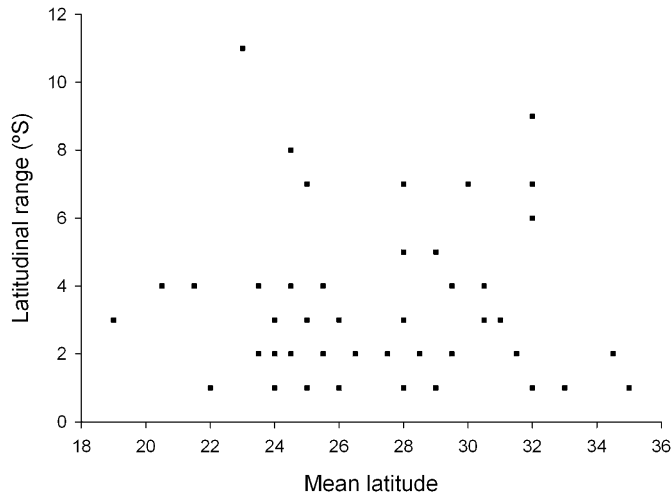


Fig. 5. Relation between median latitudinal range and latitude. Note that are some points overlap, thus making it appear that there are less than 72 points.

linear model of median latitudinal range was detected ($r^2 = 0.055$, $F = 3.83$, $P = 0.054$), while in the polynomial model the interaction was not significant ($r^2 = 0.015$, $F = 2.066$, $P = 0.155$).

The median altitudinal range and latitude were not significantly related in the linear ($r^2 = -0.006$, $F = 0.533$, $P = 0.468$) or polynomial models ($r^2 = 0.018$, $F = 0.354$, $P = 0.703$) (Fig. 6). However, we detected a significant linear association between median altitudinal range and altitude ($r^2 = 0.065$, $F = 5.983$, $P = 0.017$). The second-degree polynomial model also showed that altitudinal ranges increased with altitude with a peak at intermediate elevations ($r^2 = 0.224$, $F = 11.236$, $P < 0.001$) (Fig. 6). The interaction between latitude and altitude was not significant in the linear model ($r^2 = 0.052$, $F = 0.083$, $P = 0.775$), although they were significantly related in the second-degree polynomial model ($r^2 = 0.050$, $F = 4.702$, $P = 0.030$), suggesting that the altitudinal range of species varied with altitude in a non-linear manner along latitudinal bands.

3.4. Climatic drivers of species richness

The Simultaneous Autoregressive (SAR) model explained 56% of the variance in species richness ($F = 15.785$, $P < 0.001$) (Table 1). Of

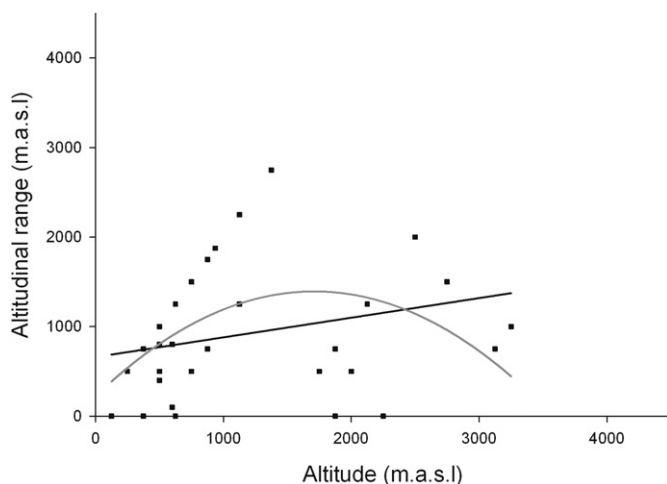


Fig. 6. Relation between median altitudinal range and altitude. The straight line shows the simple regression analysis; the curved line shows the second-degree polynomial model. Note that some points that overlap, thus making it appear that there are less than 72 points.

Table 1

Parameter estimates for explanatory variables in the SAR model.

Variables	SAR model
Elevation	-0.004**
Annual mean temperature	1.94
Mean diurnal temperature range	0.047
Isothermality	-0.212
Minimum temperature of the coldest month	2.255*
Temperature annual range	-1.152
Mean temperature of wettest quarter	0.520**
Annual precipitation	-0.01*
Precipitation seasonality	<.001
Precipitation of warmest quarter	0.007
Annual mean temperature*annual precipitation	<.001
R ²	0.567

* $P \leq 0.05$; ** $P \leq 0.001$.

the 11 explanatory variables, four were significant in the regression analysis (Table 1). The significant explanatory variables were elevation, minimum temperature of the coldest month, mean temperature of wettest quarter and annual precipitation (Table 1). The interaction between annual mean temperature and annual precipitation was not significant.

4. Discussion

The biogeographical patterns of the endemic Chilean cacti strongly support the existence of latitudinal and altitudinal gradients of endemism. The shape of the latitudinal gradient is clearly non-linear, supporting the geometric constraints hypothesis, showing a peak of endemism occurring within mid-latitudes (25°–28° S). The altitudinal species richness pattern, however, did support the Rapoport's rule hypothesis, showing a peak of endemism occurring at low altitudes (<1000 m.a.s.l.) followed by a monotonic decrease with altitude.

The latitudinal peak of species richness of cacti endemic to Chile is included in the globally recognised Central Chile endemism diversity hotspot. The presence of an endemism richness hotspot (25°–28° S), together with two separate areas of endemism between 26° and 28° S are spatially coupled with two important climatic characteristics: (i) the transitional zone between the summer and winter rainfall pattern (Houston, 2006; Latorre et al., 2002), (ii) the transitional zone between the hyper-arid and semi-arid ombrotypes of north-central Chile (Luebert and Plischoff, 2006). These climatic aspects may be a key factor for the separation of two evolutionary histories: (i) the northern species diversification (18°–26° S) and (ii) the southern biogeographic area (27°–36° S). Also both evolutionary histories might be coupled to different climatic phenomena that affect the latitudinal and altitudinal richness patterns; this is also supported by the statistical interaction between latitude and altitude in species richness (Fig. 4).

The northern species diversification may be closely associated with the Atacama aridity dynamics, largely modulated by the Pacific sea-surface temperature anomalies, which in turn have complex multiple effects such as driving the summer rainfall into the Atacama Desert and the adjacent Altiplano (Latorre et al., 2002), and closely related to slight changes in the Oceanic fog zone (Cereceda et al., 2008). Although in the hyper-arid Atacama Desert (≤ 2 mm of annual precipitations) no cacti species can be found, maximum species richness occurred in two of the $0.5 \times 0.5^\circ$ cells with very low precipitation (≤ 25 mm). Both cells are located along the coast (25–25.5° S) in an area with strong oceanic fog influence that can maintain great biodiversity in spite of the scarce precipitation (Dillon et al., 2009; Rundel et al., 1991).

Climatic zonation derives from these processes, promoting speciation within deserts (Axelrod, 1967). This mechanism could be particularly important in the Coast Range because of its complex topography. A remarkable example of this mechanism may be the diverse endemic genus *Copiapoa* Britton and Rose, comprising some 25 species, all of them restricted to the arid and semi arid Coast Range of Chile (21°–31°S). Similar species richness patterns have been observed for other arid plant species which are thought to have diversified in association with the aridity dynamics in the Atacama Desert, such as *Heliotropium* spp. (Boraginaceae), *Malesherbia* spp. (Maleshebiaceae) and *Nolana* spp. (Solanaceae) (Dillon et al., 2009; Gengler-Nowak, 2003; Luebert and Wen, 2008).

The southern biogeographic area (27°–36° S) is associated with semi-arid, xeric and pluvio-seasonal bioclimatic zones of Central Chile. In this area the most important isolation mechanism for many plant groups is thought to have been the glacial Pleistocene refuge dynamics experienced in the complex mountain chains composed by the Andes and Coast Ranges and the transverse mountain chain that crosses Central Chile. Within this area, ice sheets moved downwards from high altitudes during glacial maxima, thus isolating populations in different valleys (Bull-Hereñu et al., 2005). As annual precipitations and temperature during winter (coldest months) are critical for Cactaceae (Table 1), during glacial maxima cacti may have been confined to relict refuges. Cold has been documented as a strong barrier for Cactaceae diversity patterns in Argentina and Chile (Kraus, 1995; Mourelle and Ezcurra, 1997b). Within this southern biogeographical area the genus *Eriosyce* Phil. shows the highest species richness in the Chilean Cactaceae, suggesting that this genus is an apt candidate to test the role of glacial dynamics in speciation.

In this study we showed that geographic hard boundaries imposed in the north by the Atacama Desert, the oldest and most arid region worldwide (~150 My), and by the cold and humid conditions in the south (at least ~25 My), produced geometric constraints on latitudinal species richness driving the contemporary biogeographical patterns of the endemic Chilean cacti (Clarke, 2006; Hartley et al., 2005). One of the most remarkable constraints is the hyper-aridity observed in the Atacama Desert, because its consequences are visible in latitudinal and altitudinal patterns of endemic cactus species, which in the most northern part of Chile (i.e., 18–26° S) has produced a drastic decline in species richness between 1000 and 2750 m.a.s.l. (Fig. 4). Arroyo et al. (1988) demonstrated that the aridity of the Atacama Desert diminishes Andean plant species richness between 18° and 24° S at altitudes less than 3750 m.

The geographic constraints imposed by southern temperate conditions also decrease the endemic cacti species richness, where the mixed environmental conditions of high moisture and low temperatures, particularly during the winter, impose severe restrictions on plants with tropical biogeographic origin. Along coastal southern Chile (>36° S) no cacti can be found, whereas in the Andean Range some non-endemic species survive principally in association with Patagonian steppes (Kraus, 1995). The latitudinal mid-domain effect suggests that the Atacama Desert and the mixed environmental conditions of moisture and cold act as hard barriers in which, in a stochastic perspective, range size and range placement are governed by chance. In a deterministic perspective the Mid-domain effects in species richness patterns arise from biological responses to environmental thresholds rather than a gradual response to environmental gradients (Colwell and Lees, 2000).

Altitudinal species richness patterns suggest another type of biological response of the endemic Chilean cacti; species richness shows a sharp altitudinal gradient with richness concentrated in low elevation ranges, supporting Rapoport's rule (Fig. 3). The

proposed mechanism explaining this pattern is the existence of a highly variable environment in the higher depauperate zones, in which only species able to tolerate a wide range of climatic conditions can survive at high altitudes (Stevens, 1992). The extreme climatic conditions in high altitude zones produce multiple direct detrimental effects on plant species, diminishing their survival. Moreover, indirect synergetic effects such as depressed pollinator richness and visits relative to plant species richness and altitude can impose severe selective pressures affecting the demographic performance of cacti (Arroyo et al., 1982; Grytnes and Vetaas, 2002).

Distribution ranges of species showed a more complex pattern with wider altitudinal ranges at intermediate altitudes (Fig. 6). Five of the seven species that grow above 1600 m.a.s.l. occurred in low latitudes, their narrow altitudinal distribution range may be limited by the hyper-arid conditions. On the other hand, the three species with wider altitudinal distribution (>2.000 m of amplitude) live at intermediate latitudes without a direct influence of hyper-aridity.

An understanding of patterns of endemism is important for the establishment of criteria for conservation planning and for elucidating evolutionary mechanisms involved in the diversification of lineages with a common historical process. This study documents the presence of an endemism hotspot area within the Coast Range between 25° and 28° S, thus stressing the fact that conservation efforts should be focused primarily on this area to ensure the maximum protection for most of the endemic Chilean cacti, and the identity of the biogeographical areas with different evolutionary histories.

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Appendix. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.jaridenv.2011.04.036

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