

Latitudinal patterns and regionalization of plant diversity along a 4270-km gradient in continental Chile

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Abstract According to the global latitudinal diversity gradient, a decrease in animal and plant species richness exists from the tropics towards higher latitudes. The aim of this study was to describe the latitudinal distribution patterns of Chilean continental flora and delineate biogeographic regions along a 4270-km north–south gradient. We reviewed plant lists for each of the 39 parallels of continental Chile to build a database of the geographical distribution of vascular plant species comprising 184 families, 957 genera and 3787 species, which corresponded to 100%, 94.9% and 74.2% of the richness previously defined for Chile, respectively. Using this latitudinal presence–absence species matrix, we identified areas with high plant richness and endemism and performed a Cluster analysis using Jaccard index to delineate biogeographic regions. This study found that richness at family, genus and species levels follow a unimodal 4270-km latitudinal distribution curve, with a concentration of richness in central Chile (31–42°S). The 37th parallel south (central Chile) presented the highest richness for all taxonomic levels and in specific zones the endemism (22–37°S) was especially high. This unimodal pattern contrasts the global latitudinal diversity gradient shown by other studies in the Northern hemisphere. Seven floristic regions were identified in this latitudinal gradient: tropical (18–22°S), north Mediterranean (23–28°S), central Mediterranean (29–32°S), south Mediterranean (33–37°S), north temperate (38–42°S), south temperate (43–52°S) and Austral (53–56°S). This regionalization coincides with previous bioclimatic classifications and illustrates the high heterogeneity of the biodiversity in Chile and the need for a reconsideration of governmental conservation strategies to protect this diversity throughout Chile.

Key words: biodiversity conservation, biogeography, Chilean flora, macroecology, regionalization.

INTRODUCTION

The latitudinal diversity gradient observed by Alexander von Humboldt, more than 200 years ago, is probably the oldest and most famous observed ecological pattern (Hawkins 2001). According to this general pattern, a decline in animal and plant species richness exists from the tropics towards higher latitudes. Many reasons to explain this pattern have been hypothesized, including climate and productivity gradients, width of continents and speciation rate (Rosenzweig 1992; Gaston 1996; Hawkins 2001; Turner 2004). There is a vast amount of literature regarding world latitudinal diversity patterns in animal and plant species; however, work in the northern hemisphere comprises the majority of studies that focus on the latitudinal diversity gradient in vascular flora. For example Qian (1998, 1999) studied a >6000-km gradient ranging from

26°N to 85°N latitude in North America (north of Mexico) and found a decline in plant richness towards the poles at species and genera levels. Also in China Zhang *et al.* (2009) found a similar plant decline in species richness between 24°N and 34°N. In contrast to the northern hemisphere, there have been far fewer studies in the southern hemisphere dealing with latitudinal gradients for plant species richness, and those that exist do not show a clear north–south pattern, perhaps because of the small latitudinal range considered. For example, Fensham (1995) found a north–south vegetation change gradient (17°30'S to 22°30'S) in Australia but a weak correlation between species richness and latitude. Also, O'Brien (1993) found a west-to-east pattern for the woody flora of South Africa (15°S to 35°S), instead of a latitudinal south–north diversity pattern.

Contrary to the world latitudinal diversity pattern, along the west side of the southern cone of South America it is generally believed that a latitudinal pattern of plant species richness exists, with a

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concentration of richness in central Chile (Oberdorfer 1960; Schmithüsen 1960). The flora of continental Chile is found between 17°35'S and 56°S latitude, spanning 4270 km along a north–south axis and covering a surface area of 756 626 km². According to Marticorena (1990), the richness of vascular flora of continental Chile is represented by 5105 species, 184 families and 1008 genera, with an endemism of 45.8% (species level). Villagrán and Hinojosa (1997) estimated the forest species richness in continental Chile and found that species richness was concentrated in the central region of Chile. Recent research also supports these findings. Moreira-Muñoz and Muñoz-Schick (2007) studied the distribution of the Asteraceae family and reported that the highest genus richness is found between 33°S and 34°S. Ponce *et al.* (2002) and Rozzi *et al.* (2008) showed that the area near the 40°S latitude band contains the greatest pteridophyte richness in continental Chile. These findings all highlight central Chile as one of the world's 25 biodiversity hotspots (Myers *et al.* 2000). Nonetheless, the biodiversity distribution patterns along the north–south length of Chile have received little attention, with no representative national samples to validate the hypothesis of a concentration of the species richness in central Chile, which would contrast with the latitudinal diversity gradient found in other areas of the world.

In Chile, the geographic distribution of the vegetation is closely linked to a north–south climate gradient, which is expressed by an increase in precipitation and a decrease in temperature from north to south (di Castri & Hajek 1976). Based on the global system of bioclimatic classification (Rivas-Martínez 1993), Amigo and Ramírez (1998) proposed the existence of four major bioclimatic belts in continental Chile from north to south (tropical, Mediterranean, temperate and boreal). Luebert and Pliscoff (2006) renamed the boreal bioclimatic belt as the Austral bioclimatic belt. Under this system, the transition between climate zones is represented not just by rainfall and temperature regime changes (incorporated in the 'thermicity index'), but also by the broad-scale replacement of the vegetation communities. Thus, one could expect a close relationship between change in the geographical distribution of plant species and the boundaries of the bioclimatic belts proposed.

In this study we hypothesized that vascular richness at family, genus and species levels is concentrated in central Chile and that the vascular flora along Chile's 4270 km continental latitudinal gradient is related to different bioclimatic belts. In this context, for continental Chile, and based on a representative national sample, we aimed to (i) describe the geographic distribution patterns of the taxonomic richness, origin and life forms of the vascular flora; and (ii) delineate biogeographic regions based on the Chilean flora.

The Andean Range to the east, the Atacama Desert to the north, and the Pacific Ocean to the west and south constitute significant biogeographical barriers that have kept the flora of Chile relatively isolated from the rest of South America (Armesto *et al.* 1998). Thus knowledge of the distribution of this flora within the country can contribute to the success or failure of national conservation initiatives. In Chile, over 90% of the protected area is found south of 43°S, and therefore is outside the country's most biodiverse region (Armesto *et al.* 1998).

METHODS

Bibliographic sample and description variables

To make a representative floristic sample with empirical data at a national level, an exhaustive bibliographic review of existing floristic studies was conducted for each of the 39 Chilean degrees of latitude. Floristic studies covering three sectors along each parallel (coast, centre and Andes) were examined in order to include all of the heterogeneous environments within each parallel. Bibliographic studies located 0°25' south and north of each parallel were included within each respective parallel. If the floristic study was located between two parallels ($\pm 0^{\circ}5'$), it was included in both. Consequently, we compiled a total of 97 monographs, books and articles containing plant lists, which are listed in Appendix S1. Priority was given to the use of publications limited to well-defined areas, such as national parks or administrative regions, in order to facilitate the assignment of species lists to a specific parallel. Since information for all parallels of the country did not exist, information gaps were supplemented with species lists from the Universidad de Concepción Herbarium database (CONC). All of the data from these sources have made it possible to construct a latitudinal presence–absence matrix for 39 parallels in continental Chile (Appendix S2).

The floristic catalogue of Marticorena (1990) was used as the reference for taxonomic names. To have an actual validated taxonomic plant list all scientific names were checked using the Southern Cone Catalogue (Zuloaga *et al.* 2008). Given that this study was carried out on a country-wide geographic scale, we considered the species to be the basic taxonomic level, and thus distributions of varieties and subspecies were included in the distribution of the respective species. In addition, we assumed that the species were continuously distributed between the latitudinal limits of their range. This approach is limited by the assumption of a non-disjunctive species distribution, but this should be a greater problem only in lower taxonomic levels such as varieties or subspecies with more local distributions. The bibliographic review supplemented by the CONC database provided a final database consisting of the following variables: taxonomic level (family, genus and species); origin (native, endemic, adventive) and life form (tree, shrub, sub-shrub, annual herb, biennial herb, perennial herb).

The richness at each taxonomic level was calculated using the sum of all species, genera or families found at each degree

Table 1. Overall national values of the bibliographic sample used in this study

		Richness				
Families		Genera			Species	
184		957			3787	
		Origin				
Total	Native, <i>n</i> (%)	Endemic, <i>n</i> (%)			Adventive, <i>n</i> (%)	
3739	1917 (51.3)	1297 (34.7)			525 (14.0)	
		Life form				
Total	Trees, <i>n</i> (%)	Shrubs, <i>n</i> (%)	Sub-shrubs, <i>n</i> (%)	Annual herbs, <i>n</i> (%)	Biennial herbs, <i>n</i> (%)	Perennial herbs, <i>n</i> (%)
3208	119 (3.9)	452 (14.6)	273 (8.8)	667 (21.6)	66 (2.1)	1516 (49.0)

of latitude. For this study the term native species was used for Chilean indigenous widespread species, endemic species was used for native species restricted only to Chile, and the term adventive species was used for exotic species. The degree of endemism was determined as the percentage of endemic species with respect to total species (endemic, native and adventive) for each degree of latitude. The sample studied contained a total of 184 families, 957 genera and 3787 species at the national level (Table 1). This is the largest floristic sample ever studied in Chile. These values corresponded to 100% (families), 94.9% (genera) and 74.2% (species) of the values given by Marticorena (1990) for the Chilean vascular flora, validating the representativeness of this sample. While Marticorena (1990) proposes a 45.8% endemism in continental Chile, according to the national sample the endemism of vascular plants was approximately 34.7% of total species and 40.4%, without considering adventive species. The difference between the sample values used in this study and in Marticorena (1990) may be due to the large number of genus and family reviews carried out in the last 20 years and the fact that the list compiled did not include the surface area of the entire country. This resulted in empty areas between parallels, which were not sampled and consequently may have caused some taxa to be omitted from the study. The proportion of adventive species found in this study was about 14%. Marticorena (1990) proposes 11.4% for this category in Chile, which coincides with the results of this study. It should be noted that the origin and life form were not known for all species, and thus the total number of species used to analyse these variables does not correspond with the total number of species used for the richness analysis. Therefore, a total of 98.7% (3739 species) of the species were of known origin and 81.7% (3093 species) were of known life form.

Statistical analysis and regionalization

For the study of the distribution patterns and their respective statistical analyses we extracted the adventive species from

the total pool of the presence–absence database, so that our matrix consisted of 3214 native and endemic species. The adventive species were included in the analysis only to describe patterns on biogeographic origin. A quadratic regression model ($\text{richness} = y + a \times \text{latitude} + b \times \text{latitude}^2$) was fitted at the species, genus and family levels in order to examine whether the species richness distribution follows a latitudinal unimodal curve. In addition a correlation analysis was made between species, genus and family richness at each parallel and latitude increment until and after the parallel with greatest species richness. Significant high negative or high positive correlations would represent a continuous decrease or increase, respectively, in species richness along the latitudinal gradient from the centre of the curve.

To delineate biogeographic regions (Kreft & Jetz 2010), Jaccard distance (Mueller-Dombois & Ellenberg 1974) was selected for quantifying pairwise dissimilarities among parallels from the latitudinal species matrix. In this analysis we also excluded adventive species because of the human influence on their geographical distribution, which would introduce bias to the results. Unweighted pair-group average (UPGMA) cluster analysis using arithmetic averages was applied to the distance matrix in order to form floristic regions between latitudinal units. UPGMA is a consistent agglomerative clustering algorithm in which between-group dissimilarities are calculated as the average of all possible pairs of members of each group (Kreft & Jetz 2010). Evaluation plots (Salvador & Chan 2004; Kreft & Jetz 2010) from two different evaluation criteria were examined to delimit the number of significant clusters: (i) height of nodes in the dendrogram and (ii) total endemism (number of taxa endemic to a single biogeographical region divided by the number of non-endemic taxa). An optimal number of clusters was determined with the minimum root mean square error criterion of the L-method (Salvador & Chan 2004). For clustering, the PAST statistical package (version 2.09) was used (Hammer *et al.* 2009). After clustering, latitudes belonging to a particular group were pooled to analyse the characteristics of each new regional assemblage in terms of

the number of species, including natives, adventives, country-endemics and regional-endemics.

RESULTS

The countrywide distribution of richness at family, genus and species levels followed a unimodal curve for all taxonomic levels, with the greatest frequency concentrated in central Chile (31–42°S) and decreasing gradually towards the north and south. The 37th parallel south presented the highest richness for all three taxonomic levels (Fig. 1). Quadratic regression models resulted in highly significant fits between latitude increment and species ($r^2 = 0.83$; $P < 0.001$), genus ($r^2 = 0.88$; $P < 0.001$) and family ($r^2 = 0.92$; $P < 0.001$) richness. The unimodal distribution of richness was also validated by a highly significant positive correlation ($r = 0.70$; $P < 0.001$) between the species richness and an increment in latitude until 37°S. The same tendency was found for genera and family richness ($r = 0.81$; $P < 0.001$ and $r = 0.97$; $P < 0.001$, respectively). After 37°S there was a highly significant negative correlation ($r = -0.928$; $P < 0.001$) between these two variables. In this case, the same tendency was also found for genera and family levels ($r = -0.945$; $P < 0.001$ and $r = -0.98$; $P < 0.001$, respectively). Species richness was intermediate in the northern area (18–30°S) highest in the central area (31–42°) and lowest in the southern area (43–56°). The differences in terms of richness were greater for species and genera than for families, where the curve was ‘flatter’ (Fig. 1). Adventive species, as a single

group, followed the same unimodal distribution so that there were no major differences in the pattern by pooling adventive, native and endemic taxa together, with only a slight increase of richness along the gradient resulting from the input of more species.

Native plants were the most frequent species throughout the country with an increase of species to the south and north of the gradient (Fig. 2). Adventive species were mainly found in the central zone of Chile between 33°S and 42°S with proportions >20%, decreasing towards the north and south. In the extreme south (<53°S) the proportion of adventive species was <10%. Endemism showed a strong positive surge starting at the 22nd parallel south and reaching a maximum at 28°S (37.8%). From 37°S southward, the percentage of endemic species declined, reaching minimum values in the southernmost zone (0%). The 33rd parallel south had the greatest richness of endemic species (417 species); nonetheless, the parallel with the greatest proportion of endemic species was 28°S. The areas of greatest endemism did not coincide with the areas of greatest species richness (Fig. 1). The parallel with the highest number of native species was 37°S, but the greatest proportions of native species were found in the southernmost area (43–56°S), where over 75% of all species were native.

Specifically for native and endemic species combined, perennial herbs were the most abundant group throughout continental Chile, always comprising more than 44.7% of the species and with increasing proportions towards the south (Fig. 3). Perennial herbs were followed by annuals (17.9% nationally) and shrubs

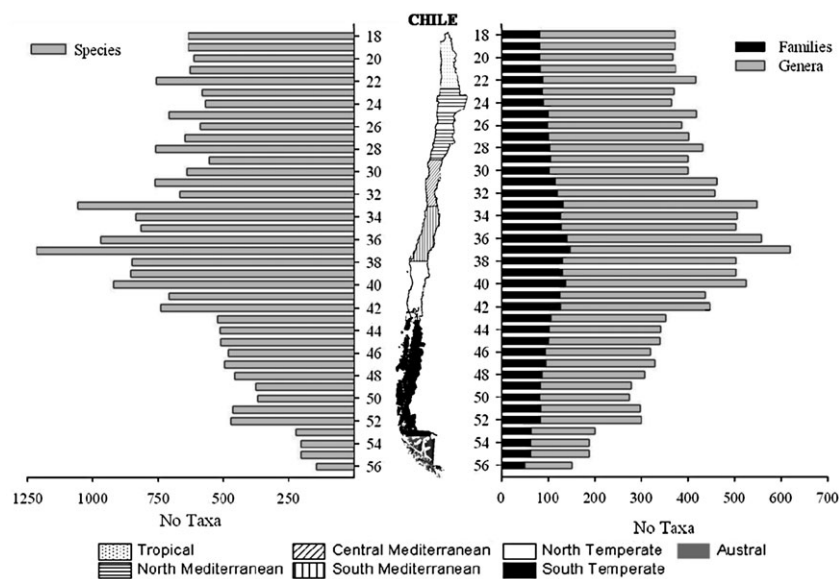


Fig. 1. Species, families and genera richness of continental Chile at each latitude (excluding adventive species). The different biogeographic regions are shown. Numbers along the y-axes denote degrees of latitude.

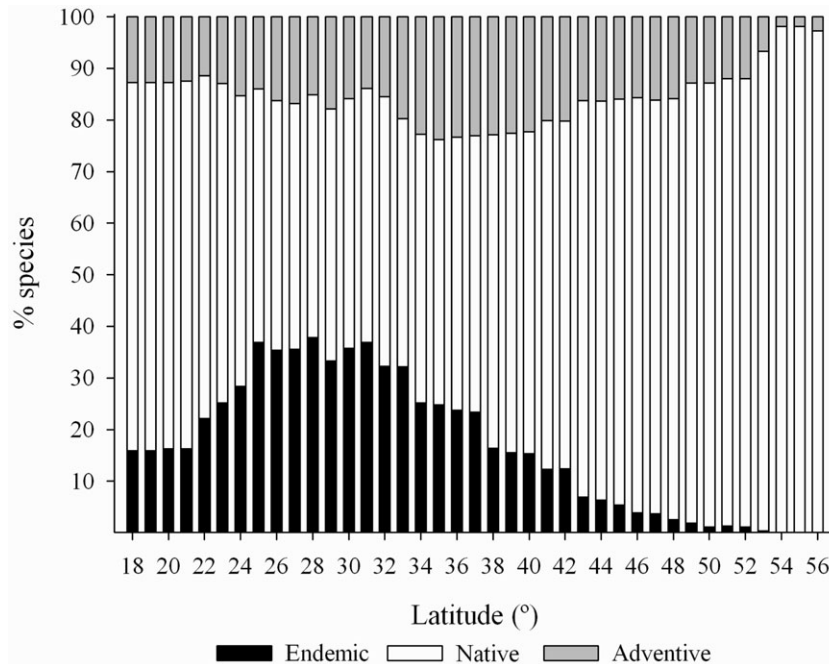


Fig. 2. Percentage of species by biogeographic origin for each latitude.

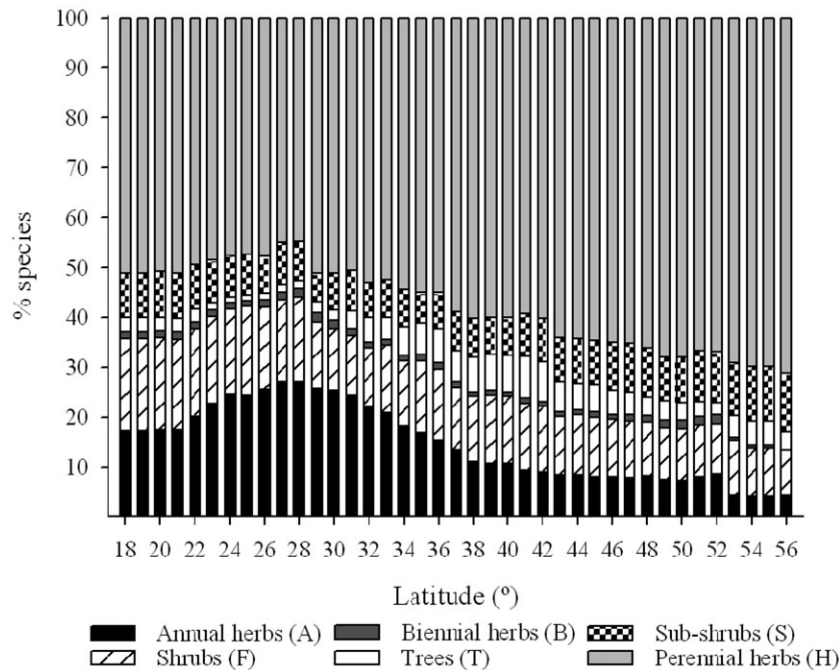


Fig. 3. Life forms of species for each degree of latitude in continental Chile (excluding adventive species).

(16.1% nationally), showing decreasing proportions with increasing latitude. Biennials with 1.1% nationally were the life form with the lowest proportion of records and almost disappeared from the 53°S parallel southward. Sub-shrubs showed consistent proportions throughout Chile, varying from 5.6% (29°S) to 11.7%

(56°S). The proportion of trees was only larger than 5% between 32°S and 45°S, peaking at 38°S and 42°S (>7%).

Cluster analysis and the L-method showed that seven floristic regions can be selected as an optimum number of groups when the height of dendrogram

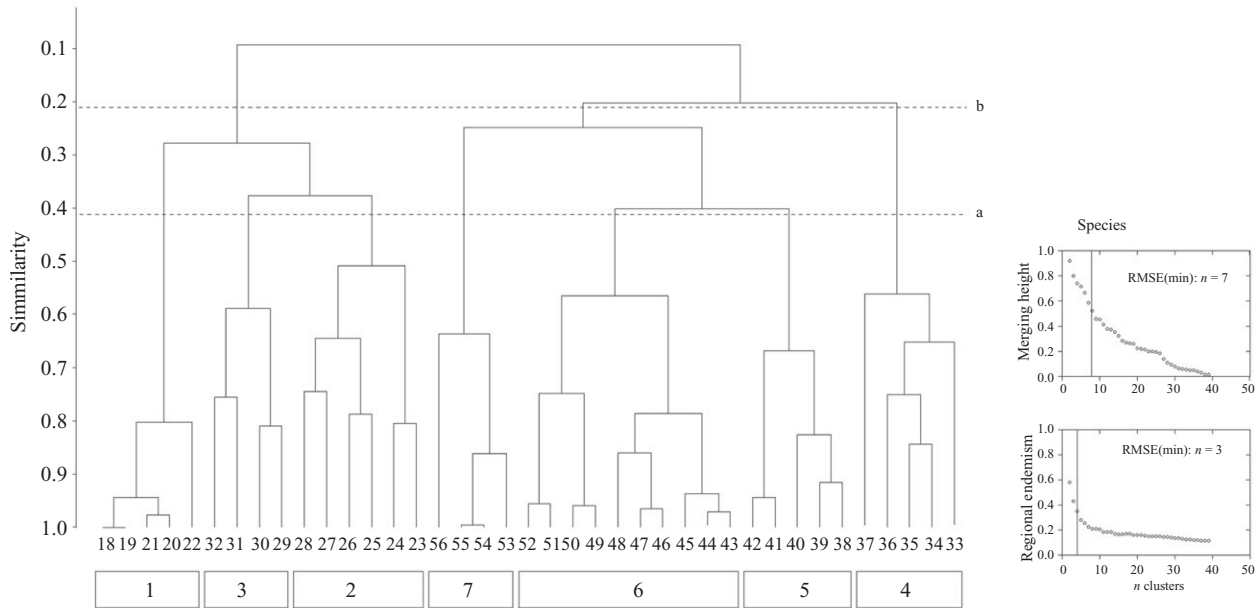


Fig. 4. Biogeographical regionalization of latitude \times species matrix using unweighted pair-group method for cluster analysis (UPGMA), resulting in a regionalization of the flora with seven floristic regions. The y-axis represents the Jaccard similarity index. The dotted lines represent the cluster cutting level according to the evaluation plots from the L-method for (a) height of nodes and (b) regional endemism (for details see *Methods*). Floristic regions: 1, Tropical; 2, North Mediterranean; 3, Central Mediterranean; 4, South Mediterranean; 5, North Temperate; 6, South Temperate; 7, Austral.

nodes is considered (Fig. 4). However, if the average proportion of endemic taxa is considered in the evaluation plot, this metric is drastically reduced to three clusters (Fig. 4). It is known that the L-method is sensitive to the curve shape, as well as to the number of taxonomical or ecological groups to be evaluated and often tends to underestimate the number of optimal clusters (Salvador & Chan 2004; Kreft & Jetz 2010). Therefore, a final decision about the optimum number of clusters or regions must be based on informative groups, for example by identifying unique assemblages (de Klerk *et al.* 2002). Thus, we selected the optimal number of clusters based on the height of nodes for constructing the regional assemblages. A description of the seven identified floristic regions is reported in Table 2 and species richness by floristic region is shown in Table 3.

DISCUSSION

Geographical distribution patterns of vascular flora in continental Chile

In this study we used a nationwide, empirical data set to show that richness at the family, genus and species levels follows a unimodal 4270 km latitudinal distribution curve. We identified the zone located between 31°S

and 42°S as the richest, with a maximum value at the 37th parallel south. This is in agreement with Hypothesis One, which stated that the greatest richness for these three taxonomic levels is found in central Chile (Oberdorfer 1960; Schmithüsen 1960). The unimodal latitudinal pattern contrasts with the global latitudinal diversity gradient shown by previous studies on vascular flora in the northern hemisphere (Qian 1998, 1999; Zhang *et al.* 2009) and in the southern hemisphere (O'Brien 1993; Fensham 1995), but is consistent with other studies in Chile (Villagrán & Hinojosa 1997; Ponce *et al.* 2002; Moreira-Muñoz & Muñoz-Schick 2007; Rozzi *et al.* 2008). Similar to Castro and Jaksic (2008), our results show that adventive species are concentrated in central Chile. These authors stressed the importance of environmental conditions and land use post-European colonization as factors that explain the non-random distribution of adventive species richness. The unimodal pattern is also followed by endemic and native species richness as independent groups. However, in terms of importance, expressed as the percentage of total species, native species are more important towards the south (Fig. 2). The same occurs with perennial herbs and shrubs, which increase their importance towards the south (Fig. 3).

The question that arises is why the vascular richness of continental Chile does not express the same pattern as in the northern hemisphere? Species richness in terms of latitudinal patterns can be explained in

Table 2. Biogeographic regions identified by this study for continental Chile and equivalence with previous classifications

Biogeographic region (this study)	Latitude (°)	Bioclimatic region (Amigo & Ramirez 1998)	Bioclimatic belt (Rivas-Martinez 1993)	Bioclimate (Luebert & Pliscoff 2006)
Tropical floristic region	18–22°S	Tropical	Thermo-tropical Meso-tropical Supra-tropical Oro-tropical Cryoro-tropical	Tropical hyperdesertic Tropical desertic Tropical xeric Tropical pluvisesonal
North Mediterranean floristic region	23–28°S	Tropical Mediterranean	Supra-tropical Thermo-Mediterranean Meso-Mediterranean	Tropical hyperdesertic Tropical desertic Tropical xeric Tropical pluvisesonal
Central Mediterranean floristic region	29–32°S	Mediterranean	Thermo-Mediterranean Meso-Mediterranean Supra-Mediterranean Oro-Mediterranean Cryoro-Mediterranean	Mediterranean hyperdesertic Tropical pluvisesonal Mediterranean hyperdesertic Mediterranean desertic-oceanic Mediterranean xeric-oceanic
South Mediterranean floristic region	33–37°S	Mediterranean Temperate	Thermo-Mediterranean Meso-Mediterranean Supra-Mediterranean Meso-temperate	Mediterranean xeric-oceanic Mediterranean pluvisesonal-oceanic
North temperate floristic region	38–42°S	Temperate	Thermo-temperate Meso-temperate	Mediterranean pluvisesonal-oceanic Temperate oceanic
South temperate floristic region	43–52°S	Temperate	Supra-temperate Meso-temperate Supra-temperate Oro-temperate Termo-boreal	Temperate hyperoceanic Temperate oceanic Temperate hyperoceanic Temperate xeric
Austral floristic region	53–56°S	Temperate Boreal	Oro-temperate Supra-temperate Thermo-boreal Meso-boreal	Temperate hyperoceanic Antiboreal hyperoceanic

Table 3. Species richness (total, natives, adventives, country-endemics, regional-endemics and regional endemism), according to biogeographical regions proposed in this study

Floristic region	1	2	3	4	5	6	7
Latitude (°S)	18–22°	23–28°	29–32°	33–37°	38–42°	43–52°	53–56°
Total species	859	1273	1054	2031	1036	819	244
Natives	574	598	487	1019	797	653	226
Adventives	98	151	122	411	284	119	17
Country-endemics	187	524	445	601	225	47	1
Regional-endemics	53	259	142	268	37	4	0
Proportion of regional endemism	0.07	0.23	0.15	0.16	0.04	0.01	0.00

1, Tropical region; 2, North Mediterranean region; 3, Central Mediterranean region; 4, South Mediterranean region; 5, North Temperate region; 6, South Temperate region; 7, Austral region.

relation to many different processes or factors (Gaston 1996). First, the transition from Mediterranean to temperate climatic belts (31–42°S) occurs in a long strip where latitudinal influences as well as altitudinal influences are recognizable. Geographically, this area has ‘U shape physiography’ formed by the Nahuelbuta Cordillera to the west (high elevation and colder areas), the ‘Depresión Intermedia’ in the centre of the country (low elevation and warmer areas) and the Andean mountain range (high elevation and colder areas). These conditions configure a heterogeneous landscape where typical Mediterranean floristic elements can reach south throughout low elevation areas until latitude 38°S (Amigo & Ramírez 1998), while floristic elements corresponding to high diversity temperate Valdivian forests reach north until temperate conditions at the Nahuelbuta cordillera in the west (latitude 37°S) and throughout the Andes mountain range in the east (latitude 35°S) (Amigo & Ramírez 1998; Amigo *et al.* 2007). This is consistent with Turner (2004), who suggests that an increase in the elevation range will result in more climatic zones, more habitats and higher species richness. Also, Rosenzweig (1992) emphasizes that as more habitats exist in a specific area higher species richness will likely be present. Thus, in central Chile a high richness of plant species adapted to the diverse climatic conditions merges in this latitudinal strip. Second, central Chile (especially the Coastal Range until the 40th parallel south) was isolated and remained free of ice during the last glaciation (ca. 15 000–20 000 BP) (Villagrán & Hinojosa 1997; Smith-Ramírez 2004), and thus served as an ecological refugium for the vascular flora of that period. In addition, this centre of high taxonomic richness helped to colonize areas south of 40°S latitude that were cleared of vegetation by the last glaciation (Smith-Ramírez 2004). In contrast, a low number of species was found south of the 43rd parallel. This might be due to the effect of the last glaciation (Villagrán & Hinojosa 1997) and due to increasing climatic harshness toward the south (temperature, rainfall and wind), resulting in a decrease in species

richness. The high species richness in the northernmost part of the country, beginning at the edge of the Atacama Desert, might be due to the great diversity of species found in the Chilean Altiplano (Highlands) (Moreira-Muñoz & Muñoz-Schick 2007).

In this study we use a very effective and practical method to describe latitudinal patterns at national or continental scales. Rosenzweig (1992) suggested that area influences latitudinal gradients because the larger the area, the greater is the variety of habitats resulting in higher species richness. In this context, one of the limitations of this study is that it was restricted only to the narrow Chilean territory and therefore did not include the complete area at these latitudes (from the Pacific to the Atlantic Ocean). It would be of great interest to apply this approach on a continental scale, to determine whether the unimodal pattern observed in Chile is applicable to the complete Southern cone of South America.

Geographical regionalization and floristic groups

We found that the distribution of the vascular flora in continental Chile is related to different bioclimatic classifications, which is consistent with our Hypothesis Two. The regionalization outlined here coincides with the bioclimatic classification proposed for Chile by Amigo and Ramírez (1998) and some transitions also proposed in Luebert and Pliscoff (2006), and Amigo *et al.* (2007), all of which were based on the Rivas-Martínez (1993) global bioclimatic model (see Table 2). According to this scheme, continental Chile contains four macroclimates distributed from north to south as tropical, Mediterranean, temperate and Austral, including many temperature and rainfall subdivisions (for details see Amigo & Ramírez 1998). In particular, the tropical to Mediterranean floristic transition coincides with the same transition proposed in Luebert and Pliscoff (2006) who split the beginning of the transition at latitude 23°S in the coastal area, from

the hyperdesertic tropical bioclimate and the hyperdesertic Mediterranean belt in the vegetational transition, from absolute-desertic to desertic shrublands (Luebert & Pliscoff 2006). However, there is a great variability in this area such that the tropical bioclimate extends up to 31°S throughout the Andean range, while at the littoral zone the climate has changed to Mediterranean because of the oceanic influence. The transition from the north Mediterranean to the central Mediterranean floristic zone is characterized by the bioclimatic transition from hyperdesertic and desertic-oceanic Mediterranean bioclimate to xeric-oceanic Mediterranean, with dominance in vegetation of desertic shrublands and lowland desertic shrublands (Luebert & Pliscoff 2006). The transition from the central Mediterranean to the south Mediterranean floristic region coincides with the transition from a xeric-oceanic to pluviseasonal-oceanic Mediterranean bioclimatic belt and the change in vegetation from desertic shrublands and lowland-desertic shrublands to a great variability of vegetation belts including spiny-shrublands, spiny-woodlands and sclerophyllous-shrublands. The south-Mediterranean floristic region maintains a stronger floristic affinity with the temperate flora than with the Mediterranean as illustrated in Figure 4 and in the characterization from Luebert & Pliscoff (2006). However, it maintains climate similarity with the Mediterranean bioclimate (Amigo & Ramírez 1998), with similar continentality index but major precipitation regimes (Luebert & Pliscoff 2006; Rivas-Martínez 2008). These major precipitation regimes may influence the presence of taller and richer vegetation types. At this transition we also found the greatest latitudinal richness in vascular flora because of a convergence between the Mediterranean and temperate flora at a heterogeneous elevation landscape. The transition from a north temperate to a south temperate floristic zone is characterized by the change from a xeric-temperate and oceanic-temperate bioclimate belt to a hyperoceanic temperate belt, and the replacement of caducifolious forests with evergreen forests (Luebert & Pliscoff 2006). The cluster at this breakpoint, however, is relatively conservative, maintaining about 40% in floristic similarity. Finally, the transition from south-temperate to Austral floristic regions coincides with the bioclimate transition from hyper-oceanic to an antiboreal hyper-oceanic bioclimatic belt and the change in vegetation from caducifolious and perennifolious forests to Tundra vegetation (Luebert & Pliscoff 2006).

In this context, our results show not only the importance of the latitudinal gradient in floristic changes, but also its importance to the individual composition of each floristic region (i.e. identity). Regional endemism (endemic species restricted to only one floristic region) is accentuated in northern latitudes, while southern floristic regions (south temperate region and

Austral region) contain almost no regional endemic plant species (Table 3). In this regard, local endemism could be the basis not only for explaining biogeographical theoretical approaches, but also for more practical disciplines such as conservation planning, and more specifically as an aide to concentrate conservation efforts (Pliscoff & Luebert 2008).

Finally, the distribution of richness throughout the different biogeographic regions of continental Chile should be taken into account when planning conservation strategies at a national level. The central-south zone of Chile (31–42°S) presents not only the greatest species richness and endemism, but also the greatest number of adventive species. Considering the few protected areas that are located in this zone and the heavy anthropogenic pressure due to 85% of the human Chilean population residing in this part of the country (INE 2004), it is apparent that there are large challenges for biodiversity conservation in central-south Chile.

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REFERENCES

- Amigo J. & Ramírez C. (1998) A bioclimatic classification of Chile: woodland communities in the temperate zone. *Plant Ecol.* **136**, 9–26.
- Amigo J., Izco J. & Rodríguez M. (2007) Bioclimatic characteristics in Chile's temperate territory. *Phytocoenologia* **37**, 739–51.
- Armesto J. J., Rozzi R., Smith-Ramírez C. & Arroyo M. T. K. (1998) Conservation targets in South American temperate forests. *Science* **13**, 1271–2.
- Castro S. & Jaksic F. (2008) Patterns of turnover and floristic similarity show a non-random distribution of naturalized flora in Chile, South America. *Rev. Chilena Hist. Nat.* **81**, 111–21.

- de Klerk H. M., Crowe T. M., Fjeldsa J. & Burgess N. D. (2002) Biogeographical patterns of endemic terrestrial Afrotropical birds. *Divers. Distrib.* **8**, 147–62.
- di Castri F. & Hajek E. (1976) *Bioclimatología De Chile*. Vicerrectoría Académica de la Universidad Católica de Chile, Santiago.
- Fensham R. J. (1995) Floristics and environmental relations of inland dry rainforest in north Queensland, Australia. *Ĵ. Biogeogr.* **22**, 1047–63.
- Gaston K. J. (1996) Biodiversity – latitudinal gradients. *Phys. Geogr.* **20**, 466–76.
- Hammer O., Harper D. & Ryan P. (2009) PAST: paleontological statistics software package for education and data analysis. *Palaeontol. Electron.* **4**, 1–9.
- Hawkins B. A. (2001) Ecology's oldest pattern? *Trends Ecol. Evol.* **16**, 470.
- INE (2004) *Resultados Generales. Censo De Población Y Vivienda 2002*. Instituto Nacional de Estadísticas (INE), Santiago.
- Kreft H. & Jetz W. (2010) A framework for delineating biogeographical regions based on species distribution. *Ĵ. Biogeogr.* **37**, 2029–53.
- Luebert F. & Plischoff P. (2006) *Sinopsis Bioclimática y Vegetacional De Chile*. Editorial Universitaria, Santiago.
- Martcorena C. (1990) Contribución a la estadística de la flora vascular de Chile. *Gayana Bot.* **47**, 85–113.
- Moreira-Muñoz A. & Muñoz-Schick M. (2007) Classification, diversity, and distribution of Chilean Asteraceae: implications for biogeography and conservation. *Divers. Distrib.* **13**, 818–28.
- Mueller-Dombois D. & Ellenberg H. (1974) *Aims and Methods of Vegetation Ecology*. John Wiley & Sons, New York.
- Myers N., Mittermeier R., Mittermeier C., Fonseca G. & Kent J. (2000) Biodiversity hotspot for conservation priorities. *Nature* **403**, 853–8.
- Oberdorfer E. (1960) Pflanzensoziologische Studien in Chile – Ein Vergleich mit Europa. In: *Flora et vegetatio Mundi 2* (eds R. Tüxen & J. Cramer) pp. 65–132. J. Cramer, Weinheim.
- O'Brien E. M. (1993) Climatic gradients in woody plant species richness: towards an explanation based on an analysis of southern Africa's woody flora. *Ĵ. Biogeogr.* **20**, 181–98.
- Plischoff P. & Luebert F. (2008) Diversidad de ecosistemas: ecosistemas terrestres. In: *Biodiversidad De Chile: Patrimonio Y Desafíos* (ed. CONAMA) pp. 74–87. Ocho Libros ediciones, Santiago.
- Ponce M., Mehltreter K. & De la Sota E. R. (2002) Análisis biogeográfico de la diversidad pteridófica en Argentina y Chile continental. *Rev. Chilena Hist. Nat.* **75**, 703–17.
- Qian H. (1998) Large-scale biogeographic patterns of vascular plant richness in North America: an analysis at the generic level. *Ĵ. Biogeogr.* **25**, 829–36.
- Qian H. (1999) Spatial pattern of vascular plant diversity in North America North of Mexico and its floristic relationship with Eurasia. *Ann. Bot.* **83**, 271–83.
- Rivas-Martínez S. (1993) Bases para una nueva clasificación bioclimática de la Tierra. *Fol. Bot. Matritensis* **10**, 1–23.
- Rivas-Martínez S. (2008) Worldwide bioclimatic classification system 1996–2009. Phytosociological Research Centre, Spain. [Updated September 2009; cited 15 May 2011.] Available from URL: <http://www.globalbioclimatics.org>
- Rosenzweig M. L. (1992) Species diversity gradients: we know more and less than we thought. *Ĵ. Mamm.* **73**, 715–30.
- Rozzi R., Armesto J. J., Goffinet B. *et al.* (2008) Changing lenses to assess biodiversity: patterns of species richness in sub-Antarctic plants and implications for global conservation. *Front. Ecol. Environ.* **6**, 131–7.
- Salvador S. & Chan P. (2004) Determining the number of cluster/segments in hierarchical clustering/segmentation algorithms. Institute of Electrical and Electronics Engineers, Piscataway. *Proceedings of the Sixteenth IEEE International Conference on Tools with Artificial Intelligence*, pp. 576–84.
- Schmithüsen J. (1960) Conifers in the forest associations of the southern Andes. *Vegetation* **9**, 313–27.
- Smith-Ramírez C. (2004) The Chilean coastal range: a vanishing centres of biodiversity and endemism in South American temperate rain forests. *Biodiv. Conserv.* **13**, 373–93.
- Turner J. R. G. (2004) Explaining the global biodiversity gradient: energy, area, history and natural selection. *Basic App. Ecol.* **5**, 435–48.
- Villagrán C. & Hinojosa L. F. (1997) Historia de los bosques del sur de Sudamérica, II: Análisis fitogeográfico. *Rev. Chilena Hist. Nat.* **70**, 241–67.
- Zhang D., Boufford D. E., Ree R. H. & Sun H. (2009) The 29°N latitudinal line: an important division in the Hengduan Mountains, a biodiversity hotspot in southwest China. *Nord. Ĵ. Bot.* **27**, 405–12.
- Zuloaga F., Morrone O. & Belgrano M. (2008) *Catálogo De Las Plantas Vasculares Del Cono Sur. Monographs in Systematic Botany 107*. Missouri Botanical Garden Press, St. Louis.

SUPPORTING INFORMATION

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

- Appendix S1.** Information sources.
- Appendix S2.** Complete data matrix.