

Classification, diversity, and distribution of Chilean Asteraceae: implications for biogeography and conservation

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ABSTRACT

This paper provides a synopsis of the Chilean Asteraceae genera according to the most recent classification. Asteraceae is the richest family within the native Chilean flora, with a total of 121 genera and c. 863 species, currently classified in 18 tribes. The genera are distributed along the whole latitudinal gradient in Chile, with a centre of richness at 33°–34° S. Almost one-third of the genera show small to medium-small ranges of distribution, while two-thirds have medium-large to large latitudinal ranges of distribution. Of the 115 mainland genera, 46% have their main distribution in the central Mediterranean zone between 27°–37° S. Also of the mainland genera, 53% occupy both coastal and Andean environments, while 33% can be considered as strictly Andean and 20% as strictly coastal genera. The biogeographical analysis of relationships allows the distinction of several floristic elements and generalized tracks: the most marked floristic element is the Neotropical, followed by the anti-tropical and the endemic element. The biogeographical analysis provides important insights into the origin and evolution of the Chilean Asteraceae flora. The presence of many localized and endemic taxa has direct conservation implications.

Keywords

Compositae, phylogeny, phytogeography, panbiogeography, synopsis Chilean flora, floristic elements, generalized tracks.

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INTRODUCTION

The Asteraceae (= Compositae) is the richest vascular plant family in the world, with 1600–1700 genera and 24,000–30,000 species (Funk *et al.*, 2005). They are easily distinguished by the florets grouped in capitula, and the fruit a cypsela often with a pappus. Asteraceae taxa can assume almost every life-form: herbs, succulents, lianas, epiphytes, trees, or shrubs, and they reach every environment and continent, except Antarctica (Funk *et al.*, 2005). Recently, there have been many improvements in the resolution of the taxonomic relationships and the classification of the Asteraceae at the subfamilial and tribal level. In the 90s the subfamily Barnadesioideae was added to the long standing subfamilies, Asteroideae and Cichorioideae (Bremer & Jansen, 1992), and more recently the classification has been updated to include 10 subfamilies and 35 tribes (Baldwin *et al.*, 2002; Panero & Funk, 2002). In contrast to the classification of subfamilies, the tribal classification of Asteraceae is old: many tribes date from the early works of Henri Cassini in the nineteenth century. The classification at the genus level is very dynamic: every year at least 10 new genera are described and many more are resurrected or moved into synonymy (Bremer, 1994). For the Chilean flora, we can mention *Xenophyllum* and *Guynesomia* as recently described genera (Funk, 1997; Bonifacino & Sancho, 2004).

Classification of the Chilean genera

Asteraceae is the family with the greatest number of genera (153) and species (1033) in the vascular flora of Chile (Marticorena, 1990). These data include introduced taxa. Taking into account only native taxa, the number of genera and species are still the highest in the Chilean flora: 121 genera and c. 863 species. According to the taxonomic proposal of Baldwin *et al.* (2002) and Panero & Funk (2002), the Chilean taxa are classified as shown in Table 1.

In Chile, 18 of 35 recognized tribes are recorded, representing 51% of the global diversity at tribal level. The tribe with the most genera in the flora of Chile is Mutisieae, with 27 genera, representing more than one-third of the tribal generic richness (Table 1). Mutisieae are followed by Astereae (18), Gnaphalieae (14), and Heliantheae (11). Tribes underrepresented in Chile are Gochnatieae and Helenieae (each one genus), and Plucheae, Tageteae, and Bahieae (each two genera). Perityleae has only two genera in Chile but it is a modest tribe of just six genera worldwide. The basal tribe (subfamily) Barnadesioideae (Barnadesioideae) is represented in Chile by three genera: *Chuquiraga*, *Dasyphyllum*, and *Doniophyton*. The phylogenetic relationships inside the subfamily are not yet well understood (Stuessy & Urtubey, 2006).

Table 1 Classification of the Chilean Asteraceae: Chilean tribes, number of genera and species, and species per genus.

Subfamily	Tribes in Chile	Total genera (global)	Total species (global)	Species per genus (global)	Chilean genera	Chilean species	Species per genus (Chile)
Barnadesioideae	Barnadesieae	9	92	10.22	3	9	3.00
Mutisioideae	Mutisieae	75	930	12.40	27	200	7.41
Gochnatioideae	Gochnatieae	6	80	13.33	1	1	1.00
Carduoideae	Cardueae	82	2500	30.49	3	10	3.33
Cichorioideae	Lactuceae	98	1550	15.82	9	59	6.56
Asteroidaeae	Senecioneae	120	3200	26.67	9	249	27.67
	Gnaphalieae	187	1250	6.68	14	71	5.07
	Astereae	174	2800	16.09	18	190	10.56
	Anthemideae	109	1740	15.96	4	8	2.00
	Plucheeae	28	220	7.86	2	2	1.00
	Helenieae	13	111	8.54	1	7	7.00
	Coreopsideae	24	505	21.04	3	10	3.33
	Tageteae	34	330	9.71	2	4	2.00
	Bahieae	18	76	4.22	2	3	1.50
	Heliantheae	189	2500	13.23	11	20	1.82
	Madieae + <i>Villanova</i>	38+1	203 + 10	5.46	4	6	1.50
	Perityleae	6	75	12.50	2	2	1.00
	Eupatorieae	170	2400	14.12	6	12	2.00
TOTAL	18	1381	20,572	14.90	121	863	7.13

The most species-rich tribe in Chile is Senecioneae (249 species), followed by Mutisieae (200) and Astereae (190). The species/genus ratio shows that the most relatively species-rich tribe is Senecioneae, with 27.67 species per genus, slightly more than the ratio from this tribe at a global scale. This is mostly due to the presence of *Senecio*, the most species-rich genus in the Chilean flora. Others like Gnaphalieae almost reach the global ratio, but most tribes have a lower relative representation in Chile. This 'impoverishment' of the Chilean Asteraceae flora is contrasted by high levels of endemism at the generic level.

Reiche (1905) made, with the knowledge of that time, an analysis of the distribution of the Chilean composites. Now it is possible to update this analysis on the basis of better taxonomic and chorological knowledge. Recently, revisions of the central Andean Asteraceae have been completed (Dillon & Sagástegui, 2001; Sklenár *et al.*, 2005), but such an effort is lacking for Chile. This is an attempt to synthesize the current knowledge of Chilean Asteraceae at the tribal and generic levels.

METHODS

The distributional data were compiled from the collections of the Chilean National Herbarium at Santiago (SGO). Maps of generic distributions were created as an 'event theme' linking the database with a base map in the program ARCVIEW 2.3. A grid of 1 latitudinal degree was created and was superposed to the dot maps. Ranges were assumed to be continuous between points, unless showing big gaps from three or more latitudinal degrees and corroborated in the literature. The database from SGO consists of around 100,000 entries, from which around 8000 correspond

to native Asteraceae. Nevertheless, it is possible that collection gaps appear, specially in more isolated parts of the country. Therefore, an exhaustive revision of available regional checklists and monographs has been made (e.g. Henríquez *et al.*, 1995; Marticorena *et al.*, 1998a, b, 2001) for completing the maximal latitudinal distribution ranges.

We categorized generic distributions in four classes: (1) genera with small ranges, recorded within only 1 degree of latitude; (2) genera with medium-small ranges of distribution from 1 to 5 latitudinal degrees; (3) genera showing medium-large distribution ranges from 5 to 15 latitudinal degrees; and (4) genera with large distributions ranging from 15 to 38 degrees of latitude. From the far north (the altiplanic Parinacota province (17°35' S) to the far south (Cabo de Hornos; 56° S), Chile encompasses 38.4 degrees of latitude.

Generic richness was calculated as the sum of all genera within each latitudinal band along continental Chile. We also evaluated the number of genera distributed in 10 degree latitudinal bands, between 17.6°–27° (arid tropical zone), 27°–37° (Mediterranean-type zone), 37°–47° (temperate zone), and 47°–56° (subantarctic zone). The database loses resolution in the altitudinal profile, nevertheless three categories can be considered: coast (C), Andes (A), or both (C/A).

Finally, to evaluate the phytogeographical relationships of the Chilean Asteraceae, the global distribution for each genus was analysed and classified into seven floristic elements (*sensu* Wulff, 1950; Qian, 1999; Sklenár & Balslev, 2007) (Table 2, see Appendix S1 in Supplementary Material). Homologous distributions were further represented by means of eight generalized tracks (*sensu* Croizat, 1958; Craw *et al.*, 1999; Katinas *et al.*, 1999; Luna

Table 2 The generic composition of floristic elements and generalized tracks in the Chilean Asteraceae.

Element	Track	Definition	No. of genera	Genera
1. Pantropical		Tropics	8	<i>Achyrocline</i> , <i>Centipeda</i> , <i>Conyza</i> , <i>Cotula</i> , <i>Mikania</i> , <i>Sigesbeckia</i> , <i>Spilanthes</i> , <i>Wedelia</i> .
2. Australasiatic	2.1 Australasiatic	Southern Hemisphere: America, Australasia	4	<i>Abrotanella</i> , <i>Lagenophora</i> , <i>Leptinella</i> , <i>Trichocline</i> .
3. Neotropical	3.1 Wide Neotropical	NW USA, México to Chile	19	<i>Ambrosia</i> , <i>Baccharis</i> , <i>Galinsoga</i> , <i>Gamochaeta</i> , <i>Heterosperma</i> , <i>Schkuhria</i> , <i>Stevia</i> , <i>Tagetes</i> , <i>Coreopsis</i> , <i>Grindelia</i> , <i>Trixis</i> , <i>Viguiera</i> , <i>Villanova</i> , <i>Haplopappus</i> , <i>Helenium</i> , <i>Verbesina</i> , <i>Erechtites</i> , <i>Ageratina</i> , <i>Chaptalia</i> .
	3.2 Andean	Costa Rica, Colombia to Chile	8	<i>Aristeguietia</i> , <i>Chuquiraga</i> , <i>Cuatrecasasiella</i> , <i>Diplostephium</i> , <i>Mutisia</i> , <i>Perezia</i> , <i>Xenophyllum</i> , <i>Werneria</i> .
	3.3 Altiplanic	Altiplano Perú, Chile, Bolivia, Argentina	17	<i>Aphyllocladus</i> , <i>Chaetanthera</i> , <i>Chersodoma</i> , <i>Helogyne</i> , <i>Leucheria</i> , <i>Lophopappus</i> , <i>Lucilia</i> , <i>Luciliocline</i> , <i>Mniodes</i> , <i>Nardophyllum</i> , <i>Nassauvia</i> , <i>Pachylaena</i> , <i>Parastrephia</i> , <i>Plazia</i> , <i>Polyachyrus</i> , <i>Proustia</i> , <i>Urmenetea</i> .
	3.4 South Amazonian	Andes and southern Amazonia	8	<i>Chevreulia</i> , <i>Dasyphyllum</i> , <i>Facelis</i> , <i>Microopsis</i> , <i>Noticastrum</i> , <i>Ophryosporus</i> , <i>Picrosia</i> , <i>Tessaria</i> .
4. Antitropical	4.1 Wide antitropical	Cool regions both hemispheres	10	<i>Adenocaulon</i> , <i>Antennaria</i> , <i>Artemisia</i> , <i>Aster</i> , <i>Erigeron</i> , <i>Hieracium</i> , <i>Hypochaeris</i> , <i>Pluchea</i> , <i>Solidago</i> , <i>Taraxacum</i> .
	4.2 Circum-Pacific	Temperate regions N America, S America and Australasia	4	<i>Flaveria</i> , <i>Gochnatia</i> , <i>Microseris</i> , <i>Soliva</i> .
	4.3 Pacific-antitropical	Chile — W USA	12	<i>Agoseris</i> , <i>Amblyopappus</i> , <i>Bahia</i> , <i>Blennosperma</i> , <i>Encelia</i> , <i>Flourensia</i> , <i>Gutierrezia</i> , <i>Lasthenia</i> , <i>Madia</i> , <i>Malacothrix</i> , <i>Perityle</i> , <i>Psilocarphus</i> .
5. South-temperate		Temperate Chile/Argentina	10	<i>Belloa</i> , <i>Brachyclados</i> , <i>Doniophyton</i> , <i>Chiliophyllum</i> , <i>Chiliotrichum</i> , <i>Eriachaenium</i> , <i>Gamochaetopsis</i> , <i>Lepidophyllum</i> , <i>Macrachaenium</i> , <i>Triptilion</i> .
6. Endemic		Continental Chile/Chilean islands	17	<i>Acrisione</i> , <i>Calopappus</i> , <i>Centaurodendron</i> , <i>Dendroseris</i> , <i>Guynesomia</i> , <i>Gypothammium</i> , <i>Leptocarpha</i> , <i>Leunisia</i> , <i>Lycapsus</i> , <i>Marticoenia</i> , <i>Moscharia</i> , <i>Oxyphyllum</i> , <i>Pleocarphus</i> , <i>Podanthus</i> , <i>Robinsonia</i> , <i>Thamnosseris</i> , <i>Yunquea</i> .
7. Cosmopolitan		Worldwide, most continents	4	<i>Bidens</i> , <i>Centaurea</i> , <i>Gnaphalium</i> , <i>Senecio</i> .

Vega *et al.*, 2000) (Table 2, see Appendix S1). Global distributions were obtained from Bremer (1994), Mabberley (1997), Baldwin *et al.* (2002), and available monographs.

RESULTS

Patterns of distribution in Chile

From the 121 genera, 16 genera (13.2%) only occur in Chile within 1 degree of latitude, e.g. *Brachyclados*, *Mniodes*, and *Chiliophyllum*, including some only recorded in one locality, e.g. *Achyrocline*, *Coreopsis*, and *Gamochaetopsis* (Fig. 1). We consider the six Chilean oceanic endemic genera (*Centaurodendron*, *Dendroseris*, *Lycapsus*, *Robinsonia*, *Thamnosseris*, and *Yunquea*) (Table 2) as part of this localized group. Nineteen genera (15.7%) have medium-small ranges of distribution, between 1 and 5 latitudinal degrees, e.g. *Erechtites*, *Mikania*, *Plazia*, and *Flourensia*. Forty genera (33%) have medium-large ranges of distribution, between 5 and 15 latitudinal degrees, e.g. *Acrisione*, *Aristeguietia*, *Belloa*,

and *Gochnatia*. Forty-six genera (38%) have large ranges of distribution, greater than 15 latitudinal degrees, e.g. *Bahia*, *Centaurea*, *Haplopappus*, and *Nassauvia*. The most widely distributed genera are *Perezia*, *Leucheria*, *Baccharis*, *Conyza*, *Gamochaeta*, and *Senecio* which occupy the whole latitudinal profile from Parinacota (17°35') to Cabo de Hornos (56°).

From the 115 continental genera, 35 (30.4%) have their mean distribution in the arid-tropical northern zone between 17.6°–27° S; 53 genera (46%) have a distribution in the central Mediterranean zone (27°–37°); 22 genera (19.1%) have a distribution in the temperate zone between 37°–47°; and only five genera (*Abrotanella*, *Eriachaenium*, *Lepidophyllum*, *Leptinella*, and *Chiliophyllum*) (4.3%) have their mean distribution in the subantarctic zone of the country (south of 47°) (Fig. 1).

The mean value for the distribution of the 115 mainland genera in the latitudinal profile is 32.01°. The generic richness for each latitudinal band shows a concentration of the genera at 33°–34° (64 genera) (Fig. 2). The genera show a decline northwards and southwards from this peak. The zone with the lowest generic

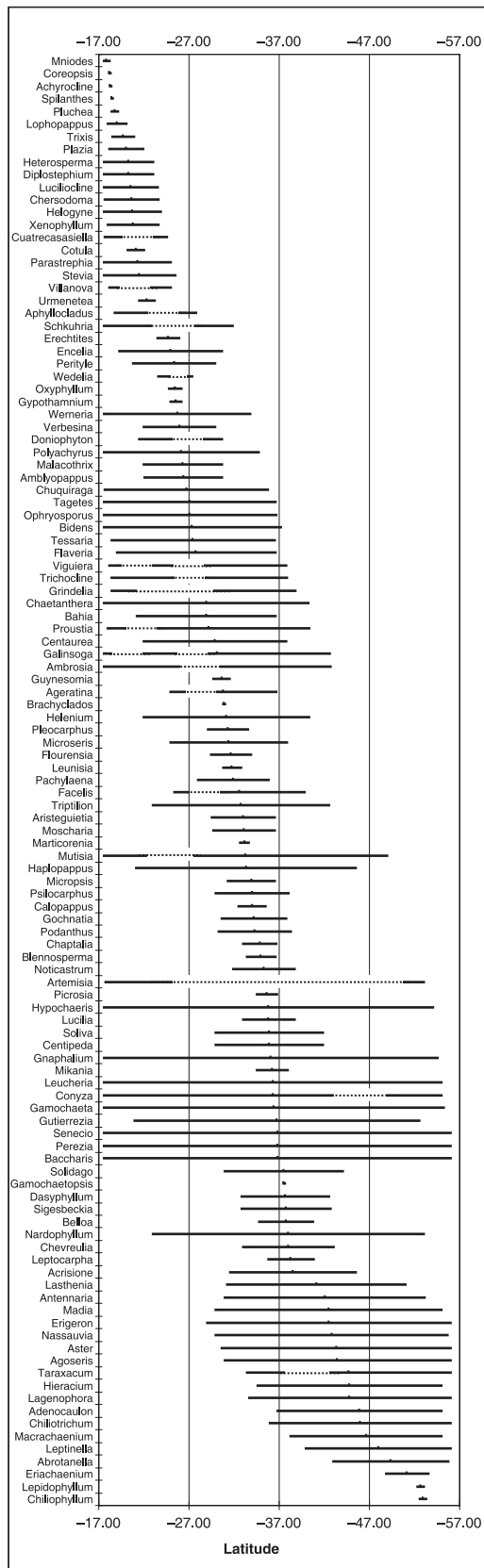


Figure 1 Latitudinal distribution of the continental Chilean Asteraceae genera (source SGO and monographs). Possible distribution or collection gaps shown as broken line.

richness occurs at the southern extreme between 55° and 56°, but still with 19 genera (Fig. 2). The decline of generic richness between 23° and 28° can be explained due to the extreme aridity conditions for plant life in the Atacama desert, the most arid of the world.

In the altitudinal profile, 38 genera (33%) were classified as Andean, and 16 as coastal (20%). But the majority ($n = 61$, or 53%) can be classified, at this low resolution, as occupying both environments. Within this latter category there are several predominantly Andean genera that reach the Pacific in Patagonia, like *Perezia* south of 45° S (Simpson, 1973).

Floristic elements and generalized tracks

Phytogeographical relationships represented by means of floristic elements and generalized tracks are shown in Table 2 and Fig. 3. The pantropical element is composed of genera that are found in all the tropics (eight genera), e.g. *Achyrocline*, *Centipeda*, and *Mikania*. The australasiatic track represents the disjunct distribution between Chile and Australasia, as shown by the four genera *Abrotanella*, *Lagenophora*, *Leptinella*, and *Trichocline*. Crisp *et al.* (1999) called this a 'South Pacific track'. The marked relationship in the Chilean Asteraceae is with the neotropics, i.e. 52 genera are classified as components of the Neotropical element. Four different tracks can be distinguished: a 'wide American', an 'Andean', an 'altiplanic', and a 'south Amazonian' track. The antitropical element is mostly referred as *amphitropical*, but several authors (e.g. Cox, 1990) have remarked that the most appropriate term would be *antitropic*, since *amphitropical* means *both tropics*. This element can be split into a 'wide antitropical track' that connects Chile with temperate North America and Eurasia (10 genera, e.g. *Adenocaulon*, *Hypochaeris*, and *Solidago*) and a 'Pacific-antitropical track' that includes most genera disjunct between central Chile and western North America (12 genera, e.g. *Bahia*, *Blennosperma*, and *Gutierrezia*). Also four genera have a distribution in western North America, South America, and Australasia (*Flaveria*, *Gochnatia*, *Microseris*, and *Soliva*) within a 'circum-Pacific track'. The austral-temperate element (10 genera) represents genera distributed only in temperate Chile and Argentina (e.g. *Chilio-phyllum*, *Eriachaenium*, and *Lepidophyllum*). The Chilean endemic element is composed of 17 genera. Six are endemic to the oceanic islands off Chile: *Lycapsus* (Perityleae) and *Thamnosseris* (Lactuceae) are restricted to the Desventuradas Islands (San Félix y San Ambrosio); *Dendroserris* (Lactuceae), *Robinsonia* (Senecio-ae) (Fig. 4), *Centauroidendron*, and *Yunquea* (both Cardueae) are restricted to the Juan Fernández archipelago. Eleven genera are endemic to mainland Chile: *Calopappus*, *Gyptothamnium*, *Leunisia*, *Marticorenia*, *Moscharia*, *Oxyphyllum*, *Pleocarpus* (Mutisieae), *Podanthus* and *Leptocarpha* (Heliantheae), *Acrisione* (Senecio-ae), and *Guynesomia* (Astereae). All of these endemic genera are monospecific or dispecific. *Gyptothamnium* and *Oxyphyllum* (Fig. 5) show a sympatric distribution around 25° S at the Atacama coast. *Calopappus*, *Guynesomia*, *Leunisia*, and *Marticorenia* are restricted to the Andes of central Chile. *Moscharia*, *Podanthus*, and *Pleocarpus* occupy both coastal and Andean environments in central Chile, while *Acrisione* and *Leptocarpha*

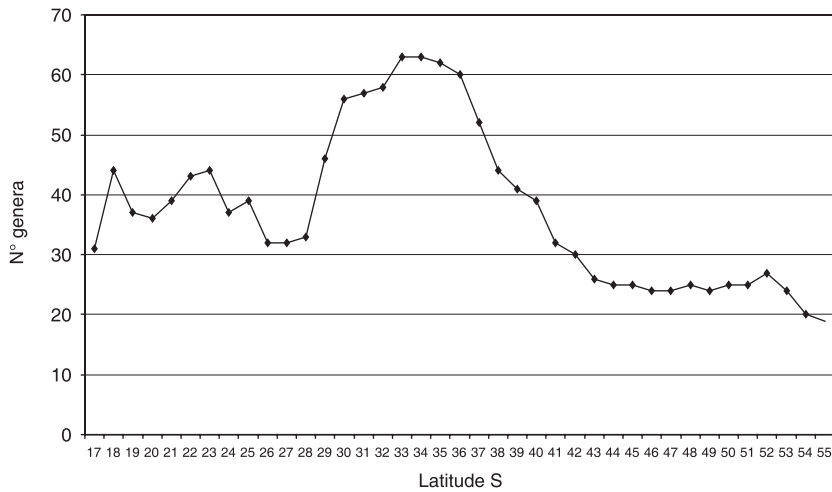


Figure 2 Generic richness in the latitudinal profile, for each one degree of latitude.

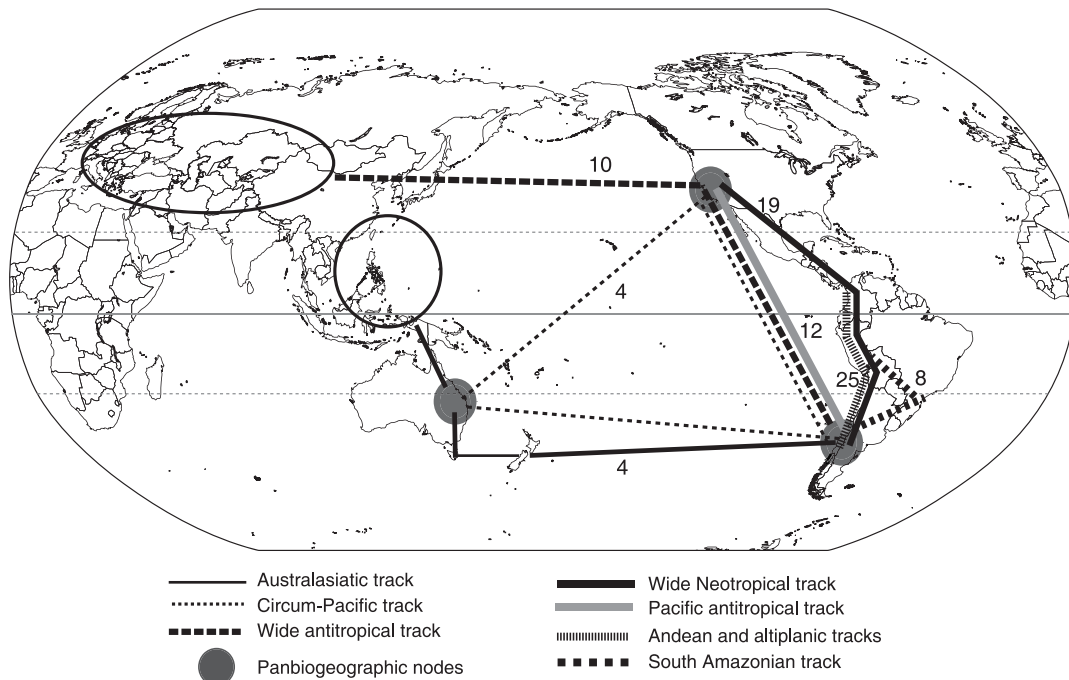


Figure 3 Generalized tracks of the Chilean Asteraceae. Possible panbiogeographical nodes (*sensu* Heads, 2004) in grey circles.

reach more temperate areas, till 45° S (Fig. 6). The highest presence of endemic genera in central Chile, and the confluence of different generalized tracks in this zone, allows to consider this as a panbiogeographical node (*sensu* Heads, 2004) (Fig. 3).

Finally, the cosmopolitan element includes four genera that can be found almost in every continent: *Bidens*, *Centaurea*, *Gnaphalium*, and *Senecio*.

DISCUSSION

Phytogeographical relationships

Floristic elements have a long history in biogeographical analysis (e.g. Wangerin, 1932; Wulff, 1950), and the most suited taxo-

nomic category for this type of analysis is the genus (Good, 1974). Therefore, the concept of geographical/floristic element has the limitation to be bounded to the taxonomic treatment, and a better understanding of the origin of a flora should include knowledge of the phylogenetic relationships (Sklenár & Balslev, 2007). Indeed, Bremer (1993) included in his analyses the sister groups of genera, tribes, and subtribes. The geographical analysis of related taxa independent of their taxonomic category is also implicit in panbiogeographical analysis (e.g. Croizat, 1958; Craw *et al.*, 1999). Heads (1999) included in his biogeographical analysis of *Abrotanella* the close related genus *Blennosperma* and the other genera in the subtribe *Blennospermatinae* that show a circum-Pacific distribution. Bremer (1993) suggests in fact that the original distribution of the Asteraceae seems to be Pacific.



Figure 4 *Robinsonia gayana*, species/genus endemic to the Juan Fernández archipelago (Photo A. Moreira-Muñoz).



Figure 5 (a) *Gybothamnium pinifolium*; (b) *Oxyphyllum ulicinum*; endemic continental species/genera at Quebrada de Ramón, Paposos, around 25° S (Photos courtesy M. Victoria Legassa).

The existence of these disjunct patterns of distribution, in taxa of diverse hierarchy, suggests vicariant processes related to the early history of the family (Bentham, 1873; Bremer, 1993; Bremer & Gustafsson, 1997; Heads, 1999; Grehan, 2007).

The circum-Pacific, australasiatic, and Pacific antitropical tracks encompass 20 genera that belong to different tribes: Anthemideae (*Leptinella*, *Soliva*); Astereae (*Centipeda*, *Gutierrezia*, and *Lagenophora*); Bahieae (*Bahia*), Gnaphalieae (*Psilocarphus*); Gochnatieae (*Gochnatiea*); Heliantheae (*Encelia* and *Flourensia*); Lactuceae (*Agoseris* and *Malacothrix*); Madieae (*Amblyopappus*, *Lasthenia*, *Madia*); Mutisieae (*Trichocline*); Perityleae (*Perityle*); Senecioneae (*Abrotanella*, *Blennosperma*); and Tageteae (*Flaveria*). Basal tribe Barnadesieae is lacking from this Pacific relationship, and Mutisieae, the sister clade to Barnadesieae (Funk *et al.*, 2005), is represented only by *Trichocline*.

Mutisieae has been considered paraphyletic and recently several groups within the tribe have been elevated to tribal or subfamily levels (e.g. Gochnatioideae) (Panero & Funk, 2002), but it still remains as the most genus-rich tribe in Chile (27 genera). Mutisieae genera reflect the general distribution of the family in Chile, with many genera restricted to the north (e.g. *Urmenetea* and *Gybothamnium*), the central (e.g. *Brachyclados* and *Marticozenia*), the south (e.g. *Eriachaenium*), as well as widely distributed genera (e.g. *Mutisia*, *Perezia*, and *Leucheria*). The phytogeographical relations emphasize the greatest number of taxa of Neotropical distribution (14), especially Andean, as well as Chilean endemics (7). The high concentration of endemic genera of Mutisieae in central Chile has been interpreted as the result of recent speciation that has led to differentiation at generic level in *Moscharia* and *Polyachyrus* that apparently descended from a Pliocene/Pleistocene ancestor, in relation to the final uplift of the Andes (Katinas & Crisci, 2000). Also in *Perezia*, the splitting of the *Prenanthoides* group into the modern two species is considered a recent Pleistocene event (Simpson, 1973). The Pleistocene has also been proposed as the period of evolution of (*Abrotanella* (Senecioneae) (Swenson & Bremer, 1997) and *Chuiriraga* (Barnadesieae) (Ezcurra, 2002).

Despite the supposedly recent evolution of the species pertaining to the latter genera, the family seems to have an ancient South American origin in relation to the Gondwana break-up (Bremer & Gustafsson, 1997). Turner (1977) suggested a Cretaceous origin for the family, and Stuessy *et al.* (1996) have suggested an origin in the early Oligocene (38 Ma) for Barnadesieae. Nevertheless, these authors recognize that the first appearance of a taxon in the fossil record does not indicate the age of origin. The earliest supposedly unequivocal fossil Asteraceae pollen has been found in Palaeocene/Eocene (55 Ma) deposits in South Africa (Zavada & de Villiers, 2000). The appearance of this pollen type in the Palaeocene–Eocene supports an early Tertiary, west Gondwana origin of the Asteraceae, but most tribes appear in the fossil record only in the middle Miocene (14 Ma) (Graham, 1996). Only by the end of Miocene (5 Ma), most of the present genera already existed (Funk *et al.*, 2005).

Recent results suggest that the most closely related families are the Calyceraceae (sister-group to Asteraceae) and Goodeniaceae (Funk *et al.*, 2005). The mainly Australian distribution of Goodeniaceae and the South American distribution of Calyceraceae support a Southern Hemisphere origin for the three families, with Goodeniaceae separated from Calyceraceae–Asteraceae when America was isolated from Australia/Antarctica (in the

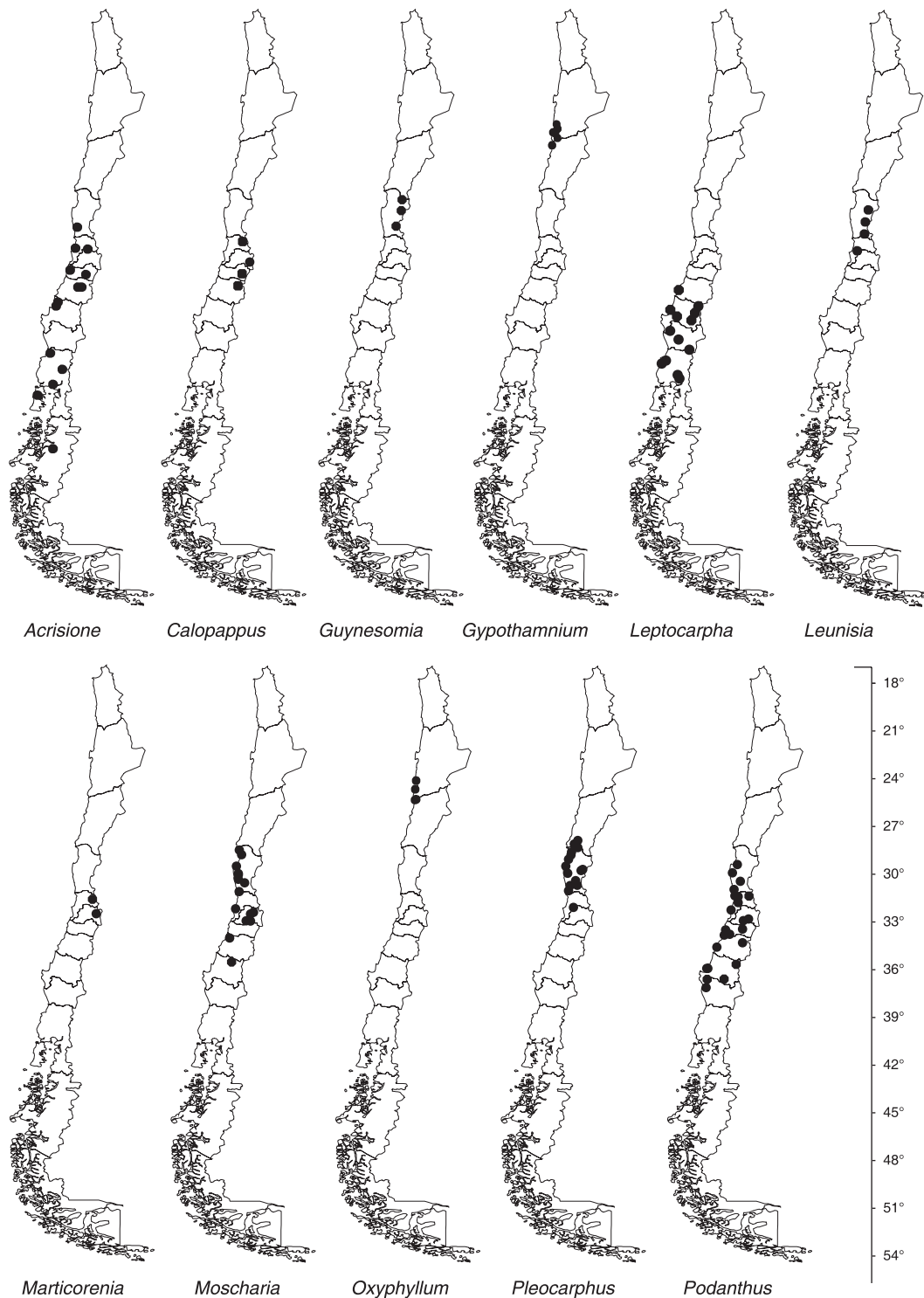


Figure 6 Distribution maps of 11 Chilean endemic Asteraceae genera (source SGO and monographs). Boundaries inside the country represent the 13 administrative regions.

early Eocene, 43–53 Ma, according to DeVore & Stuessy, 1995). The fossil pollen from South Africa (Zavada & de Villiers, 2000) is an equivocal evidence, because the old fossil records otherwise encompass both primitive clades (e.g. Mutisieae) as well as derived ones (e.g. Heliantheae). This supports an age older than the Eocene for the family (Graham, 1996).

If we accept an origin in South America for the family, there is still the question of how the family managed to occupy the rest of the world, ‘excepting Antarctica’ (Funk *et al.*, 2005). The common answer is that Asteraceae taxa have good dispersal capacity, and therefore they should have reached far territories by means of long-distance dispersal. Scenarios of long-distance dispersal

have been proposed for *Abrotanella* (Swenson & Bremer, 1997; Wagstaff *et al.*, 2006), *Hypochaeris* (Tremetsberger *et al.*, 2005), and *Microseris* (Chambers, 1963; Vijverberg *et al.*, 1999; Lohwasser *et al.*, 2004).

This does not agree with the vision of Heads (1999) and Grehan (2007). They interpret, for *Abrotanella* and *Microseris*, respectively, the Pacific disjunct pattern as the result of vicariant form-making, in relation to processes of subduction, accretion and orogenesis associated with the tectonic evolution of the Pacific region during the Mesozoic and the Palaeogene. A fact that supports the reasoning of these authors is that nine (45%) of the genera of Pacific distribution do not have a pappus suited for wind transport, i.e. for trans-oceanic dispersal (*Abrotanella*, *Blennosperma*, *Centipeda*, *Flaveria*, *Lagenophora*, *Lasthenia*, *Leptinella*, *Soliva*, and *Psilocarphus*).

The relative low percentage of cosmopolitan genera (only four) in the Chilean Asteraceae flora contrasts with the assumption that the Asteraceae have facilities of dispersion by wind or animals (Stuessy *et al.*, 1996). The perception that many Asteraceae are easily dispersed weeds conflicts with the existence of many taxa of restricted distribution (with attendant conservation problems) (Funk *et al.*, 2005). The considerable number of Asteraceae taxa naturalized in the flora of Chile, with records from the nineteenth century is without doubt due to human activities (Castro *et al.*, 2005).

Conservation implications

Small range taxa and endemics are special targets for conservation (IUCN, 2001). Indeed, almost one-third (35) of the Chilean Asteraceae genera show small to medium-small distribution ranges between just one locality to 5 latitudinal degrees. Almost half of the genera (53) have their distribution in central Mediterranean Chile from 27° to 37° S, superposed with the most human modified zone, lacking also enough protected areas (Moreira-Muñoz & Muñoz-Schick, 2003). In fact, the peak of generic richness lies at 33°–34°, the same latitudinal band where the two main cities (Santiago and Valparaíso) are located. Both cities encompass the half of the country's human population (7 million). This means a huge challenge for the conservation of these taxa (and all native organisms) in the long term. From the central Chilean endangered Asteraceae species, we have to mention *Dasyphyllum excelsum*, a crucial species from the basal Barnadesieae (Cabrera, 1959; Stuessy *et al.*, 1996). The species is long considered an endangered species at the national scale (Benoit, 1989). This latter assessment relies on a national symposium done in the 80s and recently updated (Hechenleitner *et al.*, 2005; CONAMA, 2006). A regional update has been already made for the IV Coquimbo region (29°–32° S) (Marticorena *et al.*, 2001), with the result that of the two regional extinct species, one belongs indeed to the Asteraceae (*Plazia cheiranthifolia*). The genus *Plazia* has only three species from the central Andes to Chile. Categorized as highly endangered (EP) in the region are other six Asteraceae species: *Haplopappus integerrimus*, *H. meyenii*, *Proustia pyrifolia*, *Senecio coquimbensis*, *S. munnozii*, and *Verbesina saubinetia*. Furthermore, 28 Asteraceae species have been categorized as

'vulnerable' (VU) in the region, e.g. five species of *Haplopappus*, and nine species of *Senecio*. Finally, many species are suspected to be: extinct IC(EX?) = 25; highly endangered IC(EP?) = 2; or vulnerable IC(VU?) = 49 in the region, but the limited distributional and population knowledge does not allow to categorize them satisfactorily. Similar troubling results may be expected from the assessment currently driven in the VI Region O'Higgins (34°–35° S) (Ricci, 2005), since central Chile has suffered a long history of landscape and ecosystem modifications due to human activities (Cowling *et al.*, 1996; Bustamante & Castor, 1998; Moreira-Muñoz & Muñoz-Schick, 2003).

The oceanic island taxa show an even worrying situation, since extinction rates on islands are relative higher compared with the mainland (Whittaker, 1998). From the Chilean islands, this apply specially for the taxa endemic to the Juan Fernández archipelago, that is one of the most dramatically threatened worldwide (Stuessy *et al.*, 1998). The combining invasion of browsing animals and continental plants place the island's native flora at a competitive disadvantage (Dirnböck *et al.*, 2003), so that at least 75% of the endemic flora is high threatened (Cuevas & van Leersum, 2001). The total native flora consists of 209 plant species, of which 124 are endemic, whereas the number of introduced species is 227 (Swenson *et al.*, 1997) and continue growing. The alien species does not arrive to share the limited space with the natives, but they are virtually replacing the native vegetation. Extrapolating the speed of invasion from the last 80 years for the two more invasive species (*Aristotelia chilensis* and *Ugni molinae*) suggests that 50% of the remaining montane forest could be invaded or replaced in another 80 years (Dirnböck *et al.*, 2003). Local and international efforts (Cuevas & van Leersum, 2001) to eradicate the pests have been so far not much successful, and recovery after cattle exclusion seems to be very slow (Cuevas & Le Quesne, 2006). During the twentieth century we saw the extinction of at least five species in the archipelago, e.g. *Robinsonia macrocephala*. And on August 2004 we have been testified of the extinction of the last exemplar of *Robinsonia berteroi* (Danton & Perrier, 2005). The threats follow a clear direction, being today more than 27 species in critical endangered status. Eight correspond to Asteraceae from the genera *Centaurodendron* (1), *Dendrosaris* (5), *Erigeron* (1), and *Yunquea* (1) (Danton & Perrier, 2005).

Back to the mainland, conservation research steadily suggests the need of improvement of the protected areas system in central Chile (Muñoz Pizarro, 1973; Muñoz-Schick *et al.*, 1996; Arroyo *et al.*, 2002; Plissock, 2003). A specific assessment for Chilean *Senecio* species applying Parsimony Analysis of Endemicity has been done by Rovito *et al.* (2004). This type of research barely promotes concrete conservation actions in Chile and is often uncoupled with the real problems (Prendergast *et al.*, 1999; Margules & Pressey, 2000; Moreira-Muñoz, 2005). The solutions for biodiversity conservation in Chile will not come direct from the scientific community but from an agreement between the different social stakeholders. Specially critical is the continued transformation of the sclerophyllous *matorral* into cultivation lands (Moreira-Muñoz & Muñoz-Schick, 2003), the fragmentation of the temperate forests (Echeverría *et al.*, 2006), and the rapid urbanization process (Pauchard *et al.*, 2006). The practical

improvement of biodiversity conservation in dense populated areas shows still low results, e.g. in the high populated central Chilean coast (Elórtegui, 2005).

The effectiveness of conservation efforts has not only ethical implications but practical importance for the human life (the so-called 'ecosystem services'), and not less important, the maintenance of the key taxa for our understanding of the evolution process. Specially important are the monospecific or di-specific endemic Chilean genera showing a very restricted distribution in mainland Chile or the islands. The potential extinction of any of these taxa would leave a big gap in the evolutionary chain and in our potential understanding of it, as it did the disappearing of *Robinsonia berteroi* and *Robinsonia macrocephala* from the Juan Fernández archipelago.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 Chilean Asteraceae genera, tribes, global distribution, floristic elements, tracks, altitudinal range, northern and southern distribution limits in Chile, and mean distribution. (N max = northernmost latitude, S max = southernmost latitude). Floristic elements: 1, pantropical; 2, australasiatic; 3, neotropical; 4, antitropical; 5, south-temperate; 6, endemic; 7, cosmopolitan. Generalized tracks: AUS, australasiatic; AM, wide neotropical; AN, Andean; AL, altiplanic; SA, south Amazonian; WA, wide antitropical; PA, antitropical Pacific; CP, circum-Pacific. Altitudinal range: C, coast; A, Andes; C/A, coast and Andes.

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