

## Distributional patterns of the species of *Valeriana* (Valerianaceae) in southern South America

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**Abstract** Distributional patterns of *Valeriana* species from southern South America were analyzed. We prepared a database with the records of 40 species from Argentina and Chile south of 33°S, obtained from herbarium specimens, published taxonomic studies and field trips. We undertook a track analysis and a parsimony analysis of endemism (PAE), the latter with 134 grid cells of 1.5° latitude by 1.5° longitude. Three generalized tracks and one node were obtained, and three areas of endemism were identified. These general patterns of distribution in *Valeriana* were used to infer possible vicariance and dispersal events that might have shaped them. We identified a center of diversification in Central Chile and the Argentinean province of Neuquén. It represents a complex area that is related to both the Central Chilean and Subantarctic subregions.

**Keywords** Argentina · Chile · Endemism areas · Diversification · Panbiogeography · *Valeriana*

### Introduction

Southern South America has a complex biogeographic history. The uplift of the Andes during the Tertiary and the establishment of connections between Central and South America in the Late Pliocene (3.5 mya) permitted the Andean biota to be enriched with some Nearctic floristic elements (Van der Hammen 1974; Hooghiemstra 1984; Van der Hammen and Cleef 1986; Hooghiemstra and Cleef 1995; Ricardi et al. 1997; Cody et al. 2010). The development of an arid diagonal zone from the Mid-Miocene to Late Pliocene (7–4 mya) induced the gradual isolation of the temperate forests of southern South America (Armesto et al. 1995; Aizen and Ezcurra 1998; Villagrán and Hinojosa 2005), which constitute a biogeographic island completely separated from the tropical and subtropical forests of the continent (Armesto et al. 1995). This diagonal coincides with the South American Transition Zone (Morrone 2004, 2006; Urtubey et al. 2010), representing a continuous strip of arid climate that extends along the Andes from western Venezuela and northwestern Chile, to northeastern Patagonia, in Argentina (Villagrán and Hinojosa 1997, 2005; Ezcurra 2002; Hinojosa 2004). In this transition zone should be expected marked variations in species richness as well as rapid changes in the geographical ranges of species or a combination of both (Ruggiero and Ezcurra 2003). In addition, the formation of the hyper-arid Atacama Desert in northern Chile would have prevented north-south expansion of woody elements along the Andean chain (Armesto et al. 1995; Villagrán and Hinojosa 2005). Nevertheless, several Holarctic genera of shrubs and herbs (e.g., *Astragalus*, *Berberis*, *Lupinus*, *Rubus*, *Ribes*, *Satureja* and *Valeriana*) managed to migrate from north to south (Van der Hammen and Cleef 1986; Aizen and Ezcurra 1998; Hughes and Eastwood 2006;

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Scherson et al. 2008). The repeated advances of glaciers at high latitudes during the Pliocene–Pleistocene and associated climatic changes finally contributed to shape the current distribution patterns of vegetation in Chile and Argentina (Villagrán and Hinojosa 1997, 2005). Several studies have analyzed distributional patterns of plant and animal taxa from southern South America, revealing complex biogeographic relationships that have been attributed to both vicariance and dispersal events (Morrone 1994a, 1996; Morrone et al. 1994, 1997; Posadas et al. 1997; Katinas et al. 1999; Posadas and Morrone 2003).

Valerianaceae comprise ca. 400 species (Hidalgo et al. 2004; Kutschker 2009), distributed in tropical and temperate regions of both hemispheres, with the exception of Australia and New Zealand. *Valeriana*, the most diversified and widely distributed genus within the family, is distributed in the temperate northern hemisphere, Africa and South America, the latter being an important center of diversification, especially in the North Andean Paramo (Borsini 1966; Eriksen 1989; Luteyn 1999; Bell 2004; Bell and Donoghue 2005). Pollen records (Van der Hammen 1974; Van der Hammen and Cleef 1983) indicate that *Valeriana* may have dispersed into South America through the Isthmus of Panama in the Late Pliocene (Simpson 1983; Xena de Enrech 1993) or during the Late Miocene–Early Pliocene, prior to the formation of the Isthmus, when the northwestern Andes did not present their current elevations (Bell and Donoghue 2005). South America harbors a large number of species of *Valeriana*, mainly along the Andean chain, but also in tropical, sclerophyll and rain forests, monte, steppes, and the Atlantic and Pacific coastlines. Peru is the richest country, and there are high numbers of species in Chile, Ecuador, Argentina and Colombia (Kutschker 2009). Species in the southern Andes are mostly found in mid- and low-elevation habitats, with some species restricted to the upper alpine. Species in northern Chile and northwestern Argentina are mostly inhabitants of the arid diagonal zone or areas above it, and are taxonomically related to species occurring in the northern Andes (Kutschker 2009).

Here, we use biogeographic analysis to reveal general biogeographic patterns and infer the processes associated with the complex geobiotic evolution of southern South America, using *Valeriana* as a case study. We use biogeographic methods such as track analysis (Croizat 1958, 1964; Craw et al. 1999) and parsimony analysis of endemism (Rosen 1988; Morrone 1994b) that do not require a previous phylogenetic hypothesis (Crisci et al. 2003; Morrone 2009). Although some phylogenetic analyses of Valerianaceae have been published, none of them includes *Valeriana* species that occur in the southern Andean region (Hidalgo et al. 2004; Bell and Donoghue 2005; Bell 2007; Moore and Donoghue 2007). In particular, we want to

explore the hypothesis that the wide diversification of *Valeriana* within this region has been due to both dispersal and vicariance events, which have induced biotic overlap and endemism, respectively.

## Materials and methods

The study area covers the southern region of South America, from 33° to 56° south latitude, basically corresponding to the Andean region (Morrone 2006). In Argentina it includes all the Patagonian provinces (between 62° and 74°W) and the province of Mendoza, and in Chile it extends from Region V (Valparaíso) in the north to Region XII (Magallanes) in the south (Figs. 1a, 3). This temperate area, delimited by average annual temperatures below 12°C and rainfall above 100 mm annually, is limited in the north by the South American Transition Zone (Ruggiero and Ezcurra 2003), which separates the Andean and Neotropical regions (Morrone 2004, 2006; Urtubey et al. 2010).

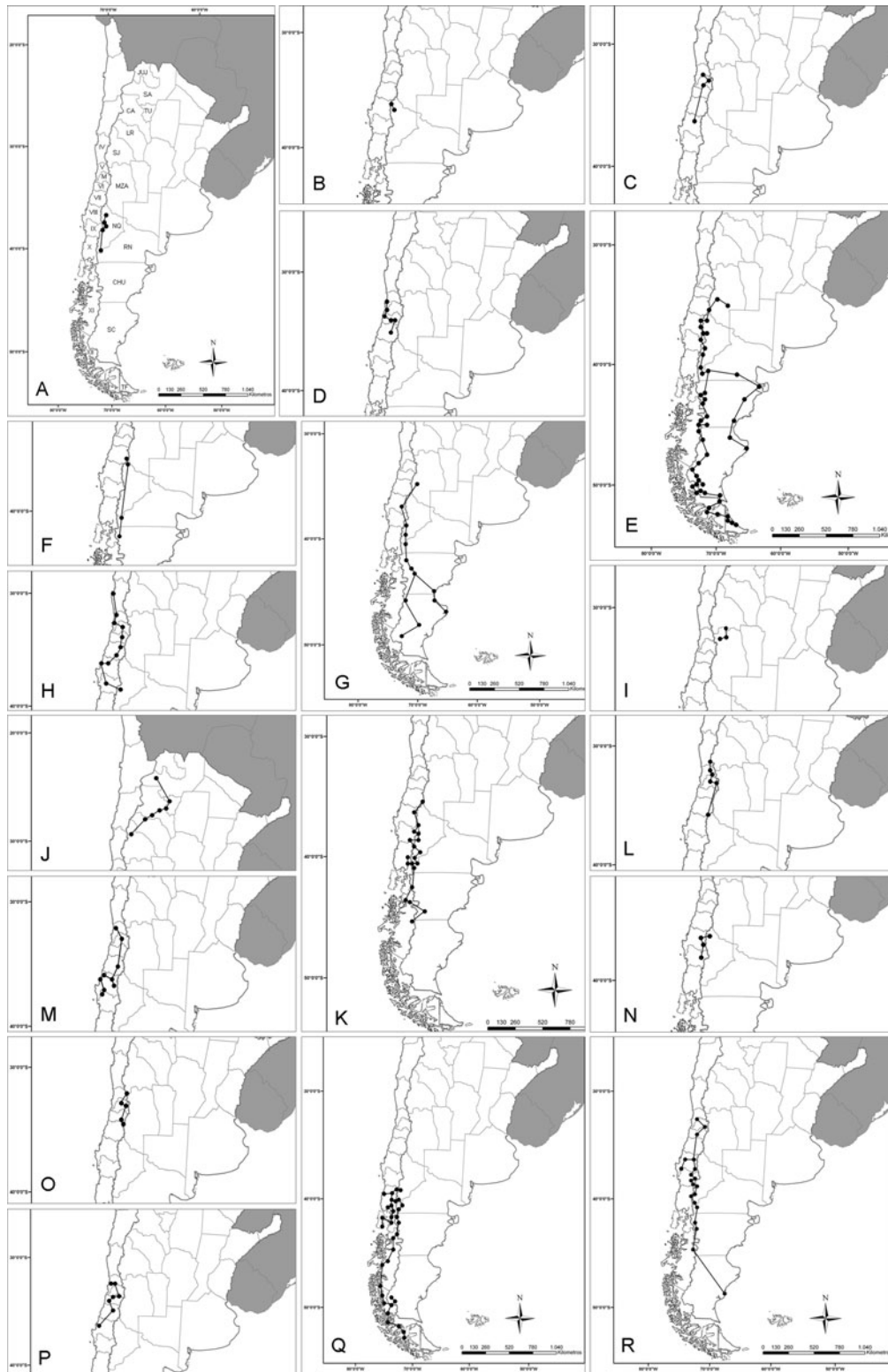
The biogeographic analyses were based on the geographical distributions of 40 species of *Valeriana*. Locality records were obtained from 1,000 specimens of the major herbaria in Argentina (BA, BAB, BCRU, LIL, LP and SI) and Chile (CONC and SGO), systematic treatments (Borsini 1944, 1946, 1966, 1999; Lörcher 1990) and field sampling. With this information we mapped the distribution of species, and conducted a track analysis and a parsimony analysis of endemism (PAE) based on grid cells (Morrone 1994b), in order to infer distributional patterns.

### Track analysis

The localities were recorded on maps and for each species an individual track was constructed, joining the localities by a minimum spanning tree (Craw et al. 1999; Crisci et al. 2003; Morrone 2009). Generalized tracks were obtained by the superposition of individual tracks of at least two taxa. These tracks represent general patterns of distribution, which could have been shaped by either vicariance or dispersal. Nodes were found in the areas of superposition of different generalized tracks.

### Parsimony analysis of endemism

We built a grid with 134 grid cells of 1.5° latitude by 1.5° longitude (“Appendix”), set from 24° to 54°S and from 76° to 57°W, starting the numbering in the southwestern sector. Scoring the presence (1) and absence (0) of the species in each grid cell, we built a data matrix (Table 1). A hypothetical grid cell, where all taxa are absent, was added to root the resulting cladograms (Morrone 1994b). The matrix



**Fig. 1** Individual tracks of *Valeriana* species. **a** *Valeriana boelckei* Rossow, **b** *V. borsinii* Rossow, **c** *V. bracteosa* Phil., **d** *V. bridgesii* Hook. & Arn., **e** *V. carnosa* Sm., **f** *V. chilensis* Borsini, **g** *V. clarionifolia* Phil., **h** *V. crista* Ruiz & Pav., **i** *V. descolei* Borsini, **j** *V. dinorrhiza* (Griseb.) Höck, **k** *V. fonckii* Phil., **l** *V. graciliceps* Clos., **m** *V. grandifolia* Phil., **n** *V. hebecarpa* DC., **o** *V. hornsuschiana* Walp., **p** *V. hyalinorrhiza*

Ruiz & Pav., **q** *V. lapathifolia* Vahl, **r** *V. laxiflora* DC. Argentinean provinces: CA Catamarca, CHU Chubut, JUJ Jujuy, LR La Rioja, MZA Mendoza, NQ Neuquén, RN Río Negro, SA Salta, SC Santa Cruz, SJ San Juan, TF Tierra del Fuego, TU Tucumán; Chilean regions: IV Coquimbo, V Valparaíso, M Metropolitana, VI O'Higgins, VII Maule, VIII Bío-Bío, IX Araucanía, X Los Lagos, XI Aisén, XII Magallanes

**Table 1** Data matrix used in the parsimony analysis of endemicity

	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
C0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C5	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C6	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C7	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0
C8	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0
C10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
C11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
C12	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
C13	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C14	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C19	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
C20	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
C21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
C22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
C23	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C24	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C25	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
C27	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0
C28	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
C29	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C32	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C34	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
C35	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
C36	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
C37	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	1	0	1
C39	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C40	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
C43	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C44	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
C45	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
C46	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0
C48	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
C49	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
C50	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0	0	1	0	1
C51	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
C54	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C56	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C58	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C59	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C62	1	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0	1	1	0	1
C63	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0
C64	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C65	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
C66	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
C67	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	1	1	0	1
C72	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C77	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 1 continued

	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
C78	1	0	0	0	1	1	1	1	0	0	1	0	0	1	0	0	0	1	0	0
C79	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0
C80	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
C81	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
C82	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	1
C83	0	1	0	0	1	0	1	0	0	0	1	1	1	0	0	0	0	1	0	1
C84	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C85	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
C87	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
C92	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C93	0	0	0	0	1	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0
C94	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	1	0	0	0	0
C95	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C96	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
C97	0	0	1	1	0	0	0	1	0	0	0	0	0	0	1	1	0	1	1	1
C98	0	0	1	1	0	0	0	1	0	0	0	1	1	0	1	0	0	1	1	0
C99	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C106	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
C107	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0
C108	0	0	1	1	0	0	0	1	0	0	0	0	1	0	0	1	0	1	0	0
C109	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
C110	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C116	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C117	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
C118	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
C119	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C120	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C122	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C125	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
C126	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
C127	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
C133	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39
C0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C3	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
C5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C6	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
C7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C13	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
C14	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C15	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
C19	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
C20	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
C21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 1 continued

	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39
C23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C25	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C29	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C30	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C32	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C34	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C35	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C36	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
C37	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
C39	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C40	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C43	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C44	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C45	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
C46	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C48	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
C49	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C50	1	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1
C51	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C54	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C56	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C58	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C59	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C62	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1
C63	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1
C64	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
C65	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1
C66	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1
C67	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1
C72	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
C77	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C78	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1
C79	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1
C80	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1
C81	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
C82	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1
C83	1	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1
C84	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C85	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
C87	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C93	1	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0
C94	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
C95	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0
C96	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C97	0	0	0	1	1	0	0	1	0	0	0	1	0	0	1	1	0	0	0	0
C98	1	0	1	0	1	0	0	0	0	1	1	1	0	0	1	1	0	0	1	0

**Table 1** continued

	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39
<b>C99</b>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<b>C106</b>	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
<b>C107</b>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	1	0	0
<b>C108</b>	0	0	0	0	1	1	0	0	0	0	0	1	0	1	1	1	0	0	1	0
<b>C109</b>	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0
<b>C110</b>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0
<b>C116</b>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
<b>C117</b>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<b>C118</b>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<b>C119</b>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0
<b>C120</b>	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0
<b>C122</b>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
<b>C125</b>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<b>C126</b>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<b>C127</b>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
<b>C133</b>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Rows are grid cells and columns are taxa (see references of species at the bottom of the table)

Species: 0, *V. boelckeii*; 1, *V. borsinii*; 2, *V. bracteosa*; 3, *V. bridgesii*; 4, *V. carnosa*; 5, *V. chilensis*; 6, *V. clarionifolia*; 7, *V. crispa*; 8, *V. descolei*; 9, *V. dinorrhiza*; 10, *V. fonckii*; 11, *V. graciliceps*; 12, *V. grandifolia*; 13, *V. hebecarpa*; 14, *V. hornsuschiana*; 15, *V. hyalinorrhiza*; 16, *V. lapathifolia*; 17, *V. laxiflora*; 18, *V. lepidota*; 19, *V. leucocarpa*; 20, *V. macrorrhiza*; 21, *V. moyanoi*; 22, *V. munozii*; 23, *V. obtusifolia*; 24, *V. papilla*; 25, *V. peltata*; 26, *V. philippiana*; 27, *V. polemoniifolia*; 28, *V. polystachya*; 29, *V. radicalis*; 30, *V. ruizlealii*; 31, *V. samolifolia*; 32, *V. sedifolia*; 33, *V. sphaerocarpa*; 34, *V. stricta*; 35, *V. vaga*; 36, *V. valdiviana*; 37, *V. velutina*; 38, *V. verticillata*; 39, *V. virescens*

was constructed with Mesquite (Maddison and Maddison 1997), and the parsimony analysis was run with TNT (Goloboff et al. 2008), performing a heuristic search with a maximum of 100 trees and 10 replicates and using a multiple search strategy TBR (tree bisection and reconnection). For the identification of the areas of endemism, we took into account only those groups of grid cells supported by at least two species (Morrone 2009).

**Results**

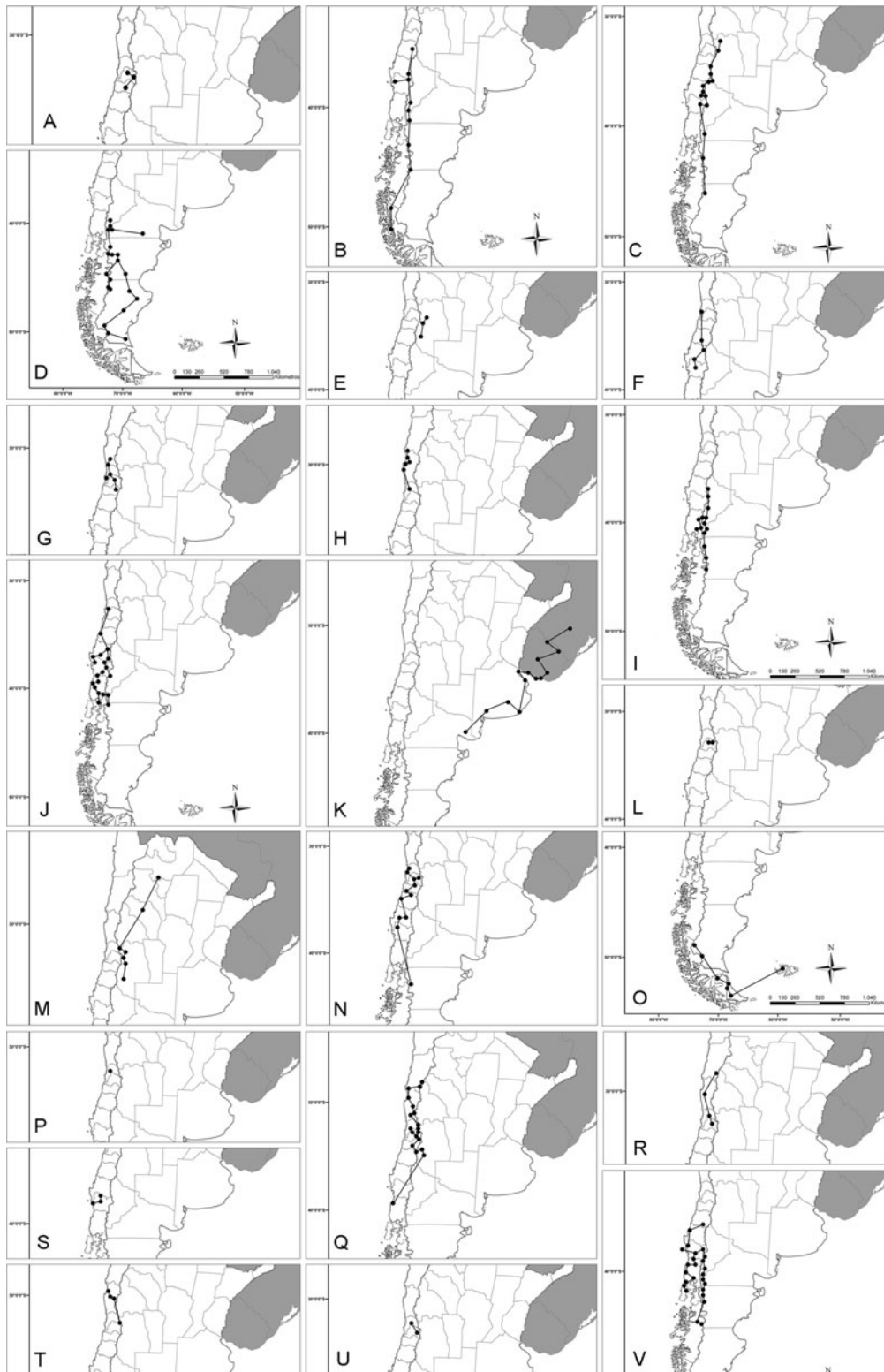
Figures 1 and 2 show the individual tracks obtained. *Valeriana radicalis* and *V. sphaerocarpa* have only been registered in two very close localities and the type locality, respectively, and therefore their individual tracks could not be obtained, although they were included in the maps (Fig. 2l, p). Most of the individual tracks are found in the Andean region (Central Chilean, Subantarctic and Patagonian subregions, according to Morrone 2006), especially in its southern sector. The individual track of *V. polystachya* (Fig. 2k) lies in the Pampa biogeographic province (Chacoan subregion, Neotropical region), which extends in central western Argentina, Uruguay and the Brazilian state of Rio Grande do Sul.

The overlap of the 38 individual tracks yielded three generalized tracks (Fig. 3): (1) Central Chilean, (2) Subantarctic in the broadest sense and (3) Prepuna,

representing a single endemic Andean pattern. The Central Chilean generalized track is defined by species endemic to Chile distributed in the western Andes from Region VII to Region IV (*V. bracteosa*, *V. bridgesii*, *V. grandifolia*, *V. hyalinorrhiza*, *V. lepidota*, *V. obtusifolia*, *V. papilla*, *V. peltata*, *V. radicalis*, *V. vaga*, *V. velutina* and *V. verticillata*). The Subantarctic generalized track is defined by species present on both sides of the Andes, and some of them are widely distributed (*V. carnosa*, *V. clarionifolia*, *V. laxiflora*, *V. polemoniifolia* and *V. virescens*), whereas other species grow exclusively in mountain areas above the tree-line (*V. boelckeii*, *V. chilensis* and *V. philippiana*). The Prepuna generalized track is defined by *V. descolei*, *V. dinorrhiza*, *V. munozii* and *V. ruizlealii*, endemic to Argentina, that are distributed from Salta to Mendoza (Figs. 1, 2). The intersection of the first two generalized tracks led to the identification of one node (Fig. 3).

**PAE**

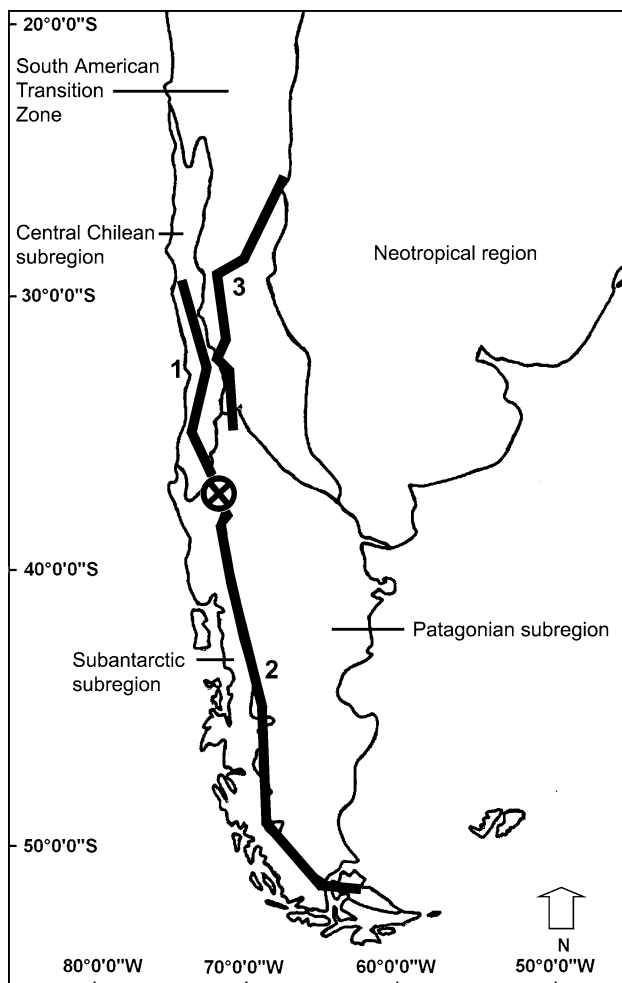
The analysis of the data matrix (Table 1) led to 10 equally parsimonious cladograms, 118 steps long, a consistency index of 0.34 and a retention index of 0.65 (Fig. 4). Three clades are supported by at least two species and are thus interpreted as areas of endemism (Fig. 5): (1) Clade A. It includes grid cells C37, C50, C62, C67, C78 and C83, and is supported by *V. laxiflora* (17), *V. leucocarpa* (19), *V. moyanoi* (21) and *V. virescens* (39). Nested within it,



**Fig. 2** Individual tracks of *Valeriana* species. **a** *Valeriana lepidota* Clos, **b** *V. leucocarpa* DC., **c** *V. macrorhiza* DC., **d** *V. moyanoi* Speg., **e** *V. munozii* Borsini, **f** *V. obtusifolia* DC., **g** *V. papilla* Bertero ex DC., **h** *V. peltata* Clos, **i** *V. philippiana* Briq., **j** *V. polemoniifolia*

Phil., **k** *V. polystachya* Sm., **l** *V. radicalis* Clos, **m** *V. ruizlealii* Borsini, **n** *V. samolifolia* (DC.) Colla, **o** *V. sedifolia* d'Urv., **p** *V. sphaerocarpa* Phil., **q** *V. stricta* Clos, **r** *V. vaga* Clos, **s** *V. valdiviana* Phil., **t** *V. velutina* Clos, **u** *V. verticillata* Clos, **v** *V. virescens* Clos





**Fig. 3** Map of the study area, showing biogeographic subregions and South American Transition Zone (*sensu* Morrone 2006). Generalized tracks and panbiogeographic node are indicated. 1 Central Chilean generalized track, 2 Subantarctic generalized track and 3 Prepuna generalized track

there is a smaller clade supported by *V. philippiana* (26) and *V. polemoniifolia* (27). (2) Clade B. It contains grids C79, C82, C94, C97, C98 and C108, and is supported by *V. grandifolia*, *V. obtusifolia* and *V. samolifolia*. It contains four nested clades (indicated in Fig. 4). (3) Clade C. It comprises grids C77 and C84, and is supported by *V. boelckei* and *V. chilensis*.

## Discussion

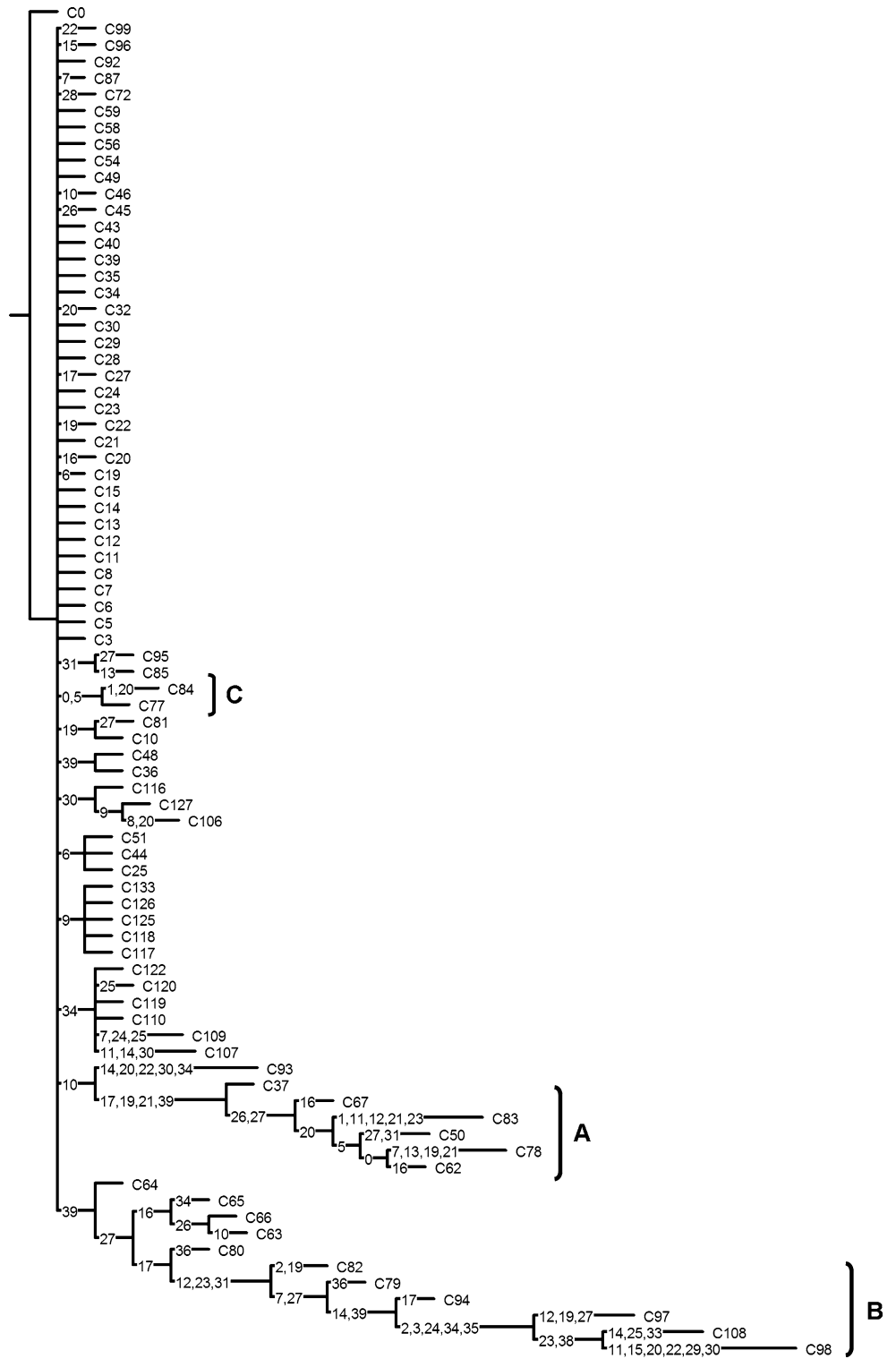
Based on the species richness and the results of the track and parsimony analyses, we postulate the existence of a center of diversification for *Valeriana* in southern South America, located in central Chile and the province of Neuquén in Argentina, where there are 25 endemic species

(Kutschker 2009). The track analysis yielded three generalized tracks. The Central Chilean track is defined by Chilean endemic species, all of them characterized by a fruit with pappus, which could have facilitated dispersal from the Andean zone to the coast and vice versa. The same type of fruit is found in the species of the Subantarctic generalized track, which are distributed in Argentina and Chile, in a wide range of ecological conditions, namely, above/below the tree-line, in lower slopes, temperate forests, foothill valleys, coastal areas and Patagonian steppe (Kutschker 2009). The Prepuna generalized track is defined by species endemic to Argentina, all of them having a fruit without pappus and a reduced dispersal capability. This track is located in the South American Transition Zone, which acted as a barrier and filter through the evolutionary biogeographic history of the flora of the South (Aizen and Ezcurra 1998; Villagrán and Hinojosa 2005), and its formation can be considered a vicariant event that has slowed the spread between the Andean and Neotropical biotas (Morrone 2004). The Prepuna continues to the north with the Puna province, which is closely related to the North Andean Paramo (Morrone 2006), another center of diversification for *Valeriana* (Eriksen 1989; Luteyn 1999; Bell and Donoghue 2005).

The Maule area (34°–37°S) was defined as a node in the track analysis. This is a complex area related to both the Central Chilean and Subantarctic subregions. Additionally, it comprises smaller areas of endemism, supported by several species. In a previous panbiogeographic analysis based on weevil taxa (Coleoptera: Curculionidae), Morrone (1996) also identified this area as a node, related to the other Subantarctic provinces and the Central Chilean subregion (Morrone et al. 1994; Morrone 2006). Moreira-Muñoz and Muñoz-Schick (2007) suggested the existence of a panbiogeographic node in this zone based on species of Asteraceae, and Rovito et al. (2004) identified a floristic boundary at 35°S approximately.

The endemic areas established in the parsimony analysis of endemicity coincided with the generalized tracks. Similar relationships have been established by Posadas et al. (1997) based on Andean vascular plants. The northern part of the Subantarctic subregion shows complex relationships with the southern part of the Central Chilean subregion. This complexity may be due to past dispersal events that involved the Maule province, where dispersal could have occurred in both directions (Posadas and Morrone 2003). The Central Chilean subregion was clearly delimited in our analysis, and its relationship with the Subantarctic subregion was also determined in previous studies (Morrone 1994a; Morrone et al. 1997). This area has been recognized as one of the world biodiversity hotspots (Arroyo et al. 1999; Myers et al. 2000).

**Fig. 4** Strict consensus cladogram obtained from a parsimony analysis of endemicity (PAE) showing relationships among the grid cells defined in the “Appendix.” Numbers refer to species supporting those clades, which are listed in Table 1



It has been suggested that the uplift of the Andes during the Neogene triggered allopatric (vicariant) diversification in plants by isolating populations on either side of the chain, and also favored the dispersal of boreotropical plant lineages from the north (Bell and Donoghue 2005; Ezcurra

et al. 2008; Antonelli et al. 2009) and provided refugia for plants during climatic fluctuations in the Pleistocene (Villagrán and Hinojosa 2005). During the Neogene, there was also a recurring pulse of warm and cold periods with the subsequent rise and fall of mountain vegetation, leading



**Fig. 5** Map showing areas of endemism A, B and C, found by the PAE

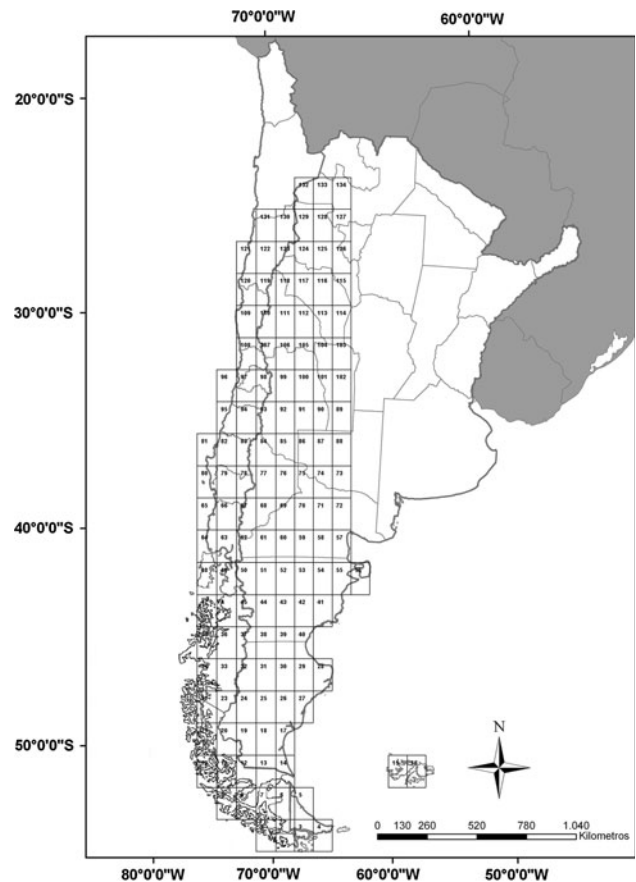
to rapid speciation and radiation (Ricardi et al. 1997; Villagrán and Hinojosa 2005). The final Andean uplift in the Late Pliocene/Pleistocene produced two severe rain shadows, one from the westerly winds resulting in the wide desert of Patagonia, and the other on the western side of the Central Andes as a result of the orographic interception of summer rainfall of Amazonian and Atlantic origin. These Neogene climatic changes on both sides of the Andes appear to have affected the biota of the southern landmasses in very different ways, according to their tectonic history and associated with a wide range of ecological conditions, under different selection pressures in the different regions (Ezcurra et al. 2008).

Our results support the hypothesis that both dispersal and vicariant processes have contributed to the wide diversification of the genus *Valeriana* in southern South America, which became a center of diversity for the genus. Diversification was especially high in the area comprising Regions VII, VIII and IX of Chile and Neuquén province in Argentina. This area consists of several areas of endemism supported by characteristic species and also harbors a panbiogeographic node relating the Central Chilean with the Subantarctic subregion.

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**Appendix**

See Fig. 6



**Fig. 6** Grid used in the parsimony analysis of endemicity, containing 134 grid cells of 1.5° latitude by 1.5° longitude

**References**

Aizen M, Ezcurra C (1998) High incidence of plant–animal mutualisms in the temperate forest of southern South America, biogeographical origin and present ecological significance. *Ecol Austral* 8:217–236

Antonelli A, Nylander JAA, Persson C, Sanmartín I (2009) Tracing the impact of the Andean uplift on Neotropical plant evolution. *Proc Natl Acad Sci USA* 106:9749–9754

Armesto JJ, Villagrán C, Arroyo MTK (eds) (1995) *Ecología de los bosques nativos de Chile*. Ed. Universitaria, Santiago de Chile

- Arroyo MTK, Rozzi JR, Simonetti J, Marquet JA, Salaberry M (1999) Central Chile. In: Mittermeier RA, Myers N, Robles-Gil P, Mittermeier CG (eds) *Hotspots: Earth's biologically richest and most endangered terrestrial ecoregions*. CEMEX-Agrupación Sierra Madre, Mexico DF, pp 161–171
- Bell CD (2004) Preliminary phylogeny of Valerianaceae (Dipsacales) inferred from nuclear and chloroplast DNA sequence data. *Mol Phylog Evol* 3:340–350
- Bell CD (2007) Phylogenetic placement and biogeography of the North American species of *Valerianella* (Valerianaceae: Dipsacales) based on chloroplast and nuclear DNA. *Mol Phylogenet Evol* 44:929–941
- Bell CD, Donoghue MJ (2005) Phylogeny and biogeography of Valerianaceae (Dipsacales) with special reference to the South American valerians. *Org Div Evol* 5:147–159
- Borsini OE (1944) Valerianaceae. In: Descole H (ed) *Gen Sp Plant Arg* 2:275–372
- Borsini OE (1946) Addenda a las Valerianáceas argentinas II. Nuevos materiales consultados. *Lilloa* 12:67–85
- Borsini OE (1966) Valerianáceas de Chile. *Lilloa* 32:375–476
- Borsini OE (1999) Valerianaceae. In: Correa MN (dir) *Flora Patagónica*. *Col Cient Inst Nac Tec Agropec* 8:448–471
- Cody S, Richardson JE, Rull V, Ellis C, Pennington RT (2010) The Great American Biotic interchange revisited. *Ecography* 33:326–332
- Craw RC, Grehan JR, Heads MJ (1999) *Panbiogeography: tracking the history of life*. Oxford Biogeography series 11, New York and Oxford
- Crisci JV, Katinas L, Posadas P (2003) *Historical biogeography: an introduction*. Harvard University Press, Cambridge
- Croizat L (1958) *Panbiogeography*. Vols. 1 and 2. Published by the author, Caracas
- Croizat L (1964) *Space, time, form: The biological synthesis*. Published by the author, Caracas
- Eriksen B (1989) Notes on generic and infrageneric delimitation in the Valerianaceae. *Nordic J Bot* 9:179–187
- Ezcurra C (2002) Phylogeny, morphology and biogeography of *Chuquiraga*, an Andean–Patagonian genus of Asteraceae–Barnadesioideae. In: Young KR, Ulloa C, Luteyn JL, Knapp S (eds.) *Plant evolution and endemism in Andean South America*. *Bot Rev* 68:153–170
- Ezcurra C, Baccalá N, Wardle P (2008) Floristic relationships among plant communities of the southern Andes and New Zealand: similarities and biogeographic implications. *Ann Bot* 101:1401–1412
- Goloboff P, Farris J, Nixon K (2008) TNT: tree analysis using new technology. Willi Hennig Society Edition. *Cladistics* 24:774–786
- Hidalgo O, Garnatje T, Susanna A, Mathez J (2004) Phylogeny of Valerianaceae based on *matK* and ITS markers with reference to *matK* individual polymorphism. *Ann Bot* 93:283–293
- Hinojosa LF (2004) Cambios climáticos y vegetacionales inferidos a partir de las paleofloras mixtas del terciario de Sudamérica. *Rev Geol Chil* 32:95–115
- Hooghiemstra H (1984) Vegetational and climatic history of the high plain of Bogotá, Colombia: a continuous record of the last 3.5 million years. *Dissert Bot* 79:368
- Hooghiemstra H, Cleef AM (1995) Pleistocene climatic change and environmental and generic dynamics in the north Andean montane forest and páramo. In: Churchill SP, Balslev H, Forero E, Luteyn JL (eds) *Biodiversity and conservation of Neotropical montane forests*. The New York Botanical Garden, New York
- Hughes C, Eastwood R (2006) Island radiation on a continental scale: exceptional rates of plant diversification after uplift of the Andes. *Proc Natl Acad Sci* 103:10334–10339
- Katinas L, Morrone JJ, Crisci JV (1999) Track analysis reveals the composite nature of the Andean biota. *Austr J Bot* 47:111–130
- Kutschker A (2009) *Valeriana* L. (Valerianaceae) en Sudamérica Austral: Taxonomía, aspectos biogeográficos y fitoquímicos. PhD Dissertation, Universidad Nacional de la Patagonia S. J. B., Comodoro Rivadavia
- Lörcher H (1990) Achsenverdickung und Sprossanatomie bei Valerianaceae. *Abh Math Naturwiss Kl Akad Wiss Mainz* 74:1–121
- Luteyn JL (1999) *Páramos: a checklist of plant diversity, geographical distribution and botanical literature*. New York Botanical Garden Press, New York
- Maddison WP, Maddison DR (1997) *Mesquite: a modular system for evolutionary analysis, version 2.5*. <http://www.mesquiteproject.org>. Accessed April 21, 2011
- Moore BR, Donoghue MJ (2007) Correlates of diversification in the plant clade Dipsacales: geographic movement and evolutionary innovations. *Amer Nat* 170:S29–S55
- Moreira-Muñoz A, Muñoz-Schick M (2007) Classification, diversity, and distribution of Chilean Asteraceae: implications for biogeography and conservation. *Divers Distrib* 13:818–828
- Morrone JJ (1994a) Distributional patterns of species of Rhytirrhini (Coleoptera: Curculionidae) and the historical relationships of the Andean provinces. *Global Ecol Biogeogr Lett* 4:188–194
- Morrone JJ (1994b) On the identification of areas of endemism. *Syst Biol* 43:438–441
- Morrone JJ (1996) Distributional patterns of the South America Aterpini (Coleoptera: Curculionidae). *Rev Soc Entomol Argent* 55:131–141
- Morrone JJ (2004) Panbiogeografía, componentes bióticos y zonas de transición. *Rev Bras Entomol* 48:149–162
- Morrone JJ (2006) Biogeographic areas and transition zones of Latin America and the Caribbean islands based on panbiogeographic and cladistic analyses of the entomofauna. *Annu Rev Entomol* 51:467–494
- Morrone JJ (2009) *Evolutionary biogeography: an integrative approach with case studies*. Columbia University Press, New York
- Morrone JJ, Roig-Juñent S, Crisci JV (1994) Cladistic biogeography of terrestrial Subantarctic beetles (Insecta: Coleoptera) from southern South America. *Natl Geogr Soc Res Explor* 10:104–115
- Morrone JJ, Katinas L, Crisci V (1997) A cladistic biogeographic analysis of Central Chile. *J Compar Biol* 2:25–41
- Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. *Nature* 403:853–858
- Posadas P, Morrone JJ (2003) Biogeografía histórica de la familia Curculionidae (Coleoptera) en las subregiones Subantártica y Chilena Central. *Rev Soc Entomol Argent* 62:75–84
- Posadas P, Estévez JM, Morrone JJ (1997) Distributional patterns and endemism areas of vascular plants in the Andean subregion. *Fontqueria* 48:1–10
- Ricardi M, Gaviria J, Estrada J (1997) La flora del superpáramo venezolano y sus relaciones fitogeográficas a lo largo de los Andes. *Plantula* 1:171–187
- Rosen BR (1988) From fossils to earth history: applied historical biogeography. In: Myers AA, Giller PS (eds) *Analytical biogeography: an integrated approach to the study of animal and plant distributions*. Chapman and Hall, London, New York, pp 437–481
- Rovito SM, Arroyo MTK, Plissock P (2004) Distributional modelling and parsimony analysis of endemism of *Senecio* in the Mediterranean-type climate area of Central Chile. *J Biogeogr* 31:1623–1636
- Ruggiero A, Ezcurra C (2003) Regiones y transiciones biogeográficas: Complementariedad de los análisis en biogeografía histórica y ecológica. En: Morrone JJ, Llorente Bousquets J (eds) *Una perspectiva latinoamericana de la biogeografía*. Las Prensas de Ciencias, UNAM, Mexico DF

- Scherson RA, Vidal R, Sanderson MJ (2008) Phylogeny, biogeography, and rates of diversification of New World *Astragalus* (Leguminosae) with an emphasis on South American radiations. *Am J Bot* 95:1030–1039
- Simpson B (1983) An historical phytogeography of the High Andean flora. *Rev Chil Hist Nat* 56:109–122
- Urtubey E, Stuessy TF, Tremetsberger K, Morrone JJ (2010) The South American biogeographic transition zone: an analysis from Asteraceae. *Taxon* 59:505–509
- Van der Hammen T (1974) The Pleistocene changes of vegetation and climate in tropical South America. *J Biogeogr* 1:3–26
- Van der Hammen T, Cleef AM (1983) Datos para la historia de la flora andina. *Rev Chil Hist Nat* 56:97–107
- Van der Hammen T, Cleef AM (1986) Development of the high Andean paramo flora and vegetation. In: Vuilleumier F, Monasterio M (eds) High altitude tropical biogeography. Oxford University Press, Oxford
- Villagrán C, Hinojosa LF (1997) Historia de los bosques del sur de Sudamérica: Análisis fitogeográfico. *Rev Chil Hist Nat* 70:241–267
- Villagrán C, Hinojosa LF (2005) Esquema biogeográfico de Chile. In: Llorente Bousquets J, Morrone JJ (eds) Regionalización biogeográfica en Iberoamérica y tópicos afines. Las Prensas de Ciencias, UNAM, Mexico DF
- Xena de Enrech N (1993) Contribución al estudio del género *Valeriana* L. en Venezuela: Distribución geográfica, caracteres morfoanatómicos, cariológicos y palinológicos de interés taxonómico y evolutivo. *Acta Bot Venez* 16:105–136