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ORIGINAL ARTICLE

Phylogenetics and predictive distribution modeling provide insights into the geographic divergence of *Eriosyce* subgen. *Neoporteria* (Cactaceae)

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Abstract The classification of *Eriosyce* subgenus *Neoporteria* (“subsection” in the sense of Kattermann) and the role of allopatry/sympatry in the diversification of the group were studied by use of cladistic and predictive distribution modeling methods. We reconstructed the phylogenetic relationships of subgenus *Neoporteria* by analyzing 38 morphological characters and DNA sequences from two chloroplast regions of 21 taxa from the Chilean subsections of *Eriosyce* using a Bayesian and maximum likelihood phylogenetic framework. Also, we attempted to find out if the divergence between the sister taxa in the *Neoporteria* group had been caused by allopatric or sympatric mechanisms. The morphology-based analysis placed *E. chilensis* basal within the *Neoporteria* clade and suggested a further broadening of the group by including *E. taltalensis* var. *taltalensis*, formerly considered a member of subsection *Horridocactus.* However, the combined DNA data placed *E. sociabilis* and *E. taltalensis* var. *taltalensis* within the *Horridocactus* clade, and placed *E. chilensis* with *E. subgibbosa* var. *litoralis.* The broad concept of *E. subgibbosa* sensu Kattermann (comprising seven infraspecific taxa), was rejected by our combined molecular results. Finally, our results corroborated changes in subsection *Neoporteria* proposed by various authors and suggested further modifications within *Neoporteria.* The analyses of the degree of geographic overlap of the predicted distributions indicated null overlap between the sister taxa, and one probable hybrid origin of *E. chilensis*, indicating that evolutionary divergence is mainly caused by an allopatric process associated with climatic tolerance.

Keywords Chile · Morphology · Diversification · Ecological niche modeling · Vicariance · Speciation

Introduction

Understanding the processes that lead to the origin of new taxa is a fundamental objective of evolutionary biology (Darwin 1859; Futuyma 2005). In this sense, the essential role of geographic isolation driving divergence of taxa had become widely accepted by the mid-20th century (Mayr 1959). Recently, new support for sympatric speciation mediated by disruptive phenotypic selection exerted by pollinators challenged geographic isolation as the single force driving the formation of new lineages (Schemske and Bradshaw 1999; Turelli et al. 2001; Fitzpatrick and Turelli 2006; Savolainen et al. 2006). Moreover, the chance of sympatric speciation in organisms with a low mobility (for example plants) is higher, and it also increases the possibility of making accurate inferences of the geography of speciation (Losos and Glor 2003). For example, if two sister plant species (both with limited seed dispersal) are distributed allopatrically, it is plausible to conclude that their divergence mechanism must be associated with geographic isolation (Barraclough and Vogler 2000; Losos and

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Glor 2003), whereas growing in sympatry ecological mechanisms, for example pollinator guilds, might account for their divergence (Schemske and Bradshaw 1999). A key issue highlighted by speciation biologists is the relevance of studying the process of divergence in a lineage-based concept (Wiens 2004a), linking methodological tools that enable understanding of the mechanism(s) underlying the evolutionary and the ecological processes that split an ancestral species into new lineages (Wiens 2004b). These views may be addressed by use of phylogenetic tools and predictive distribution modeling methods accounting for geographic dimensions of evolution (Graham et al. 2004; Kozak and Wiens 2006; Posadas et al. 2006; Katinas and Crisci 2008; Evans et al. 2009). Moreover, predictive distribution modeling has also demonstrated its utility by helping to solve problems arising from early stages of divergence or postspeciation, distinguishing cryptic species linages when morphological differences are subtle, overlapping, or not yet fixed (Raxworthy et al. 2007), because it provides evidence for geographic isolation between populations, and hence provides evidence for these populations being viewed as separate evolving lineages when gene flow is considered unlikely for the intervening unsuitable region (Graham et al. 2004; Wiens and Graham 2005; Raxworthy et al. 2007; Evans et al. 2009).

Eriosyce sensu lato (=sensu Kattermann) is a large South American genus of subglobular, globular or elongated cacti belonging to tribe Notocacteae and comprising some 30 species in its current circumscription (Kattermann 1994; Anderson 2001; Hoffmann and Walter 2004; Hunt et al. 2006). Most of its members occur in Chile between latitudes 18° and 36° S, but also in southern Peru between 14° and 18° S and in western Argentina from 24° to 37° S. In 1994, Kattermann proposed this broad concept of *Eriosyce,* amplifying the genus by including the former genera *Horridocactus*, *Islaya*, *Neoporteria*, *Pyrrhocactus*, and *Thelocephala*. *Eriosyce* sensu lato is divided into section *Eriosyce*, comprising the subsections *Eriosyce* sensu stricto (endemic to Chile), *Pyrrhocactus* (endemic to Argentina), and *Islaya* (extinct in the wild in northern Chile but frequent in southern Peru) and section *Neoporteria* (all taxa endemic to Chile) comprising subsections *Neoporteria*, *Horridocactus*, and *Chileosyce*. While this broad concept of the genus *Eriosyce* is widely used (but see Zuloaga et al. 2008), Kattermann's infrageneric and infraspecific classification of *Eriosyce* has been challenged by several authors (Nyffeler and Eggli 1997, 2010; Hunt 2003; Ferryman 2003; Hoffmann and Walter 2004; Hunt et al. 2006; Walter and Mächler 2006; Walter 2008).

Subsection *Neoporteria* is one of the most conspicuous groups within *Eriosyce* sensu lato and is mainly distributed in coastal areas, but sometimes also in transversal valleys with coastal influence between the latitudes of 27° and 36° S. With the exception of *E. chilensis*, its narrow funnelform to tubular fuchsia-colored flowers are hummingbird-pollinated and their stems become elongated with age—sometimes up to 1 m in length. *Neoporteria* occupies areas with elevated oceanic influence in the southerly Atacama Desert and the Mediterranean zones of Chile (Luebert and Pliscoff 2006). Some taxonomic proposals were based on incomplete taxa sampling and they used a limited number of floral characters that made it difficult to define infrageneric and interspecific limits, and several phylogenetic aspects remained unsolved.

In this study we examine the specific and infraspecific classification of subsection *Neoporteria* and test the hypothesis of its monophyly against members from the other Chilean subsections of *Eriosyce* sensu lato. We attempted to determine the infrageneric position of *E. chilensis* and *E. taltalensis* within *Eriosyce* sensu lato by using molecular and morphological data. Because none of the previous taxonomic or phylogenetic proposals have been spatially evaluated, thus providing little evidence for geographic isolation between sister taxa or the process of ongoing evolutionary divergence, we attempted to elucidate the role of allopatry/sympatry in the divergence found within subsection *Neoporteria* by comparing the predicted distribution overlap between sister taxa using predictive distribution modeling.

Materials and methods

Plant material

The morphological dataset was obtained by measuring at least 20 individuals in the field in *Neoporteria* sensu stricto, the *E. taltalensis* complex, and the specimens detailed in Table 1. We measured 10 individuals of each species of the other Chilean subsections of *Eriosyce*. In the case of *E. islayensis* (a taxon extinct in the wild in Chile) we used material grown from documented habitat seed (FK 895 = Fred Kattermann) and data taken from literature; data for *C. brevistylus* were taken from cultivated ex-habitat specimens. Most of the characters of the epidermis, hypodermis, cortex, and pith were adopted from Nyffeler and Eggli (1997).

Taxon sampling

The sampling of the *Eriosyce* taxa used in this study was based on the classification in Kattermann (1994, 2001) because it is widely used and enabled us to make comparisons with the first phylogenetic hypothesis proposed for *Eriosyce* sensu lato. Twelve distinct operational taxonomic

Table 1 List of taxa, their infragenerneric categories used in Kattermann (1994), their acronyms used in the cladistic and distribution modeling analyses, their latitudinal distribution in Chile, and the plant material used in this study

Species	Acronyms	Latitudinal distribution	Collection data
Outgroups			
Corryocactus brevistylus (K. Schumann) Britton and Rose	C_brevistylus	18°–20° S	HW 74 (CONC) [JF975686, JF975703], Región de Tarapacá, west of Chusmiza. F. Ritter 122 a (SGO), Región de Tarapacá, Camiña
Neowerdermannia chilensis Backeb.	Neo_chilensis	17°–18° S	HW 860 (CONC) [–, JF975704], Región de Tarapacá, Socoroma 3200 m. F. Ritter 199 (SGO), Región de Tarapacá, Chapiquiña.
Subsection ***Eriosyce***			
E. aurata (Pfeiff.) Backeb.	E_aurata	27°–33° S	HW 17 (CONC) [JF975687, JF975706], Región de Coquimbo, Fray Jorge.
Subsection ***Horridocactus***			
E. curvispina var. *curvispina* (Bertero ex Colla) Katt.	E_curvispina_cur	30°–35° S	HW 23 (CONC) [JF975689, JF975708], Región Metropolitana, El Volcan.
E. odieri subsp. *odieri* (Lem. ex Salm-Dyck) Katt.	E_odieri_odi	27° S	HW 119 (CONC) [–, JF975711], Región de Atacama, Puerto Viejo.
Eriosyce taltalensis (Hutchison) Katt. subsp. *paucicostata* (F.Ritter) Katt.	E_tal_pau	24°–25° S	HW 237 a (CONC) [–, JF975705], Región de Antofagasta, north of Paposo. HW 94, Región de Antofagasta, east of Paposo; HW 422, Region de Antofagasta, east of Taltal. F. Ritter (SGO), Región de Antofagasta, 22 km north of Paposo.
E. taltalensis (Hutchison) Katt.	E_tal_tal	25°–27° S	FK 1061 (SGO), Región de Antofagasta, Esmeralda. Eggli 2922 (CONC, SGO), Región de Antofagasta, near Taltal branching of the Quebrada Los Changos and Quebrada Los Andes. HW 253 (CONC) [JF975701, JF975724], Región de Antofagasta, Esmeralda. HW 754, Región de Antofagasta, north of Paposo. HW 400, Región de Antofagasta, Barquito
E. taltalensis (Hutchison) Katt. subsp. *pilispina* (F.Ritter) Katt.	E_tal_pil	26° S	HW 415, Región de Atacama, above Barquito, 500 m. HW 545 (CONC) [–, JF975722], Región de Atacama, 5 km east of Obispito.
E. taltalensis (Hutchison) Katt. var. *pygmaea* (F.Ritter) Katt.	E_tal_pyg	26°–27° S	HW 398 (CONC) [–, JF975723], Región de Atacama, Pan de Azúcar. HW 103, Región de Atacama, north of Chañaral. HW 227, Región de Atacama, Las Conchillas. HW 379, Región de Atacama, Morro Copiapó.
Subsection ***Islaya***			
E. islayensis (C.F. Förster) Katt.	E_islayensis	14°–18° S	FK 895 (CONC) [JF975690, JF975709], Southern Perú, Arequipa. Specimen grown from habitat seed.
Subsection ***Chileosyce***			
E. krausii (F. Ritter) Katt.	E_krausii	26° S	F. Ritter 502 (SGO), Región de Atacama, north of Caldera. HW 262 (CONC) [–,JF975710], Región de Atacama, north of Flamenco. HW 265, Region de Atacama, Porto Fino. HW 736, Región de Atacama, Pan de Azucar.
Ingroup			
Subsection ***Neoporteria***			
E. chilensis (Hildm. ex K. Schumann) Katt.	E_chilensis	32° S	FK 3 (SGO) (Neotype), Región de Valparaíso, Los Molles. FK 192 (SGO), Región de Coquimbo, Pichidangui. Eggli and Leuenberger 2931 (CONC), Región de Valparaíso, Los Molles. Eggli and Leuenberger 2934 (CONC), Región de Coquimbo, Pichidangui. HW 609 (CONC) [JF975688, JF975707], Región de Coquimbo, south of Pichidangui.
E. senilis subsp. *coimasensis* (F. Ritter) Katt.	E_senilis_coi	32° S	FK 266 (SGO), Región de Valparaíso, Las Coimas. HW 9 (CONC) [JF975691, JF975712], Región de Valparaíso, Las Coimas.
E. senilis subsp. *senilis* (Backeb.) Katt.	E_senilis_sen	30°–32° S	FK 29 (SGO), Región de Coquimbo, 43 km east of La Serena. FK 418 (SGO), Región de Coquimbo, Cuncumen. FK 422 (SGO) (Neotype), Región de Coquimbo, West of Coyton (sic) = Coirón. FK 423 (SGO), Región de Coquimbo, Quelen. FK 452 (SGO), Región de Coquimbo, Huampulla. FK 462 (SGO), Región de Coquimbo, El Tambo. Eggli and Leuenberger 2553 (SGO), Región de Coquimbo, Cuesta El Espino. HW 636 (CONC) [JF975692, JF975713], Región de Coquimbo, Huampulla.

Table 1 continued

Species	Acronyms	Latitudinal distribution	Collection data
E. sociabilis (F. Ritter) Katt.	E_sociabilis	27° S	FK 147 (SGO) (Neotype), Región de Atacama, Totoral Bajo.
			FK 803 (SGO), Región de Atacama, Morro Copiapó.
			HW 279 (CONC) [JF975693, JF975714], Región de Atacama, south of Totoral Bajo.
			HW 387, Región de Atacama, north of Caldera.
			HW 526, Región de Atacama, east of Obispito.
			HW 646, Región de Atacama, north of Totoral Bajo.
E. subgibbosa (Haw.) Katt.	E_subgibbosa_sub	32°–36° S	FK 207 (SGO), Región de Coquimbo, 10 km north of Valparaíso.
			Eggli and Leuenberger 2938 (CONC), Región de Coquimbo, Pichidangui.
			Eggli, Leuenberger and Arroyo-Leuenberger 3089 (SGO), Región de Coquimbo, Caleta Oscuro.
			Eggli, Leuenberger and Arroyo-Leuenberger 3104 (CONC), Región de Valparaíso, Quinteros.
			Eggli and Leuenberger 3109 (CONC), Región de Valparaíso, El Quisco.
			Eggli, Leuenberger and Arroyo-Leuenberger 3119 (CONC), Región del Libertador General Bernardo O'Higgins, Punta de Lobos.
			Eggli, Leuenberger and Arroyo-Leuenberger 3122 (CONC), Región del Libertador General Bernardo O'Higgins, Bucalemu.
			Eggli, Leuenberger and Arroyo-Leuenberger 3123 (CONC), Región del Libertador General Bernardo O'Higgins, Bucalemu.
			Eggli, Leuenberger and Arroyo-Leuenberger 3134 (CONC), Región del Maule, Limpimávida.
			K. Behn s.n. (CONC), Región de Coquimbo, Cerro La Cruz. K. Behn s.n. (CONC), Región de Valparaíso, Concón.
			HW 147 (CONC), Región de Valparaíso, south of Valparaíso.
			HW 594, Región del Maule, south of Constitución.
			HW 645, Región de Coquimbo, Confluencia.
			HW 214 [JF975698, JF975719], Región del Libertador General Bernardo O'Higgins, Punta de Lobos.
E. sugibbosa var. *castanea* (F. Ritter) Katt.	E_sugibbosa_cas	34°–35° S	FK 202 (SGO), Región del Libertador General Bernardo O'Higgins, Santa Cruz.
			Eggli, Leuenberger and Arroyo-Leuenberger 3139 (CONC), Región del Maule, 18 km south of San Javier.
			FK 204 (SGO), Región del Maule, Villa Prat.
			HW 34 (CONC) [JF975694, JF975715], Región del Maule, Villa Prat.
			HW s.n., Región del Libertador General Bernardo O'Higgins, Tuna.
			HW 155, Región del Maule, Litú.
E. subgibbosa var. *litoralis* (F.Ritter) Katt.	E_subgibbosa_lit	29°–31° S	HW 47 (CONC), Región de Coquimbo, Totoralillo.
			HW 65 Región de Coquimbo, south of Chungungo.
			HW 619 [JF975696, JF975717] Región de Coquimbo, north of Los Vilos.
E. subgibbosa subsp. *clavata* (Söhrens ex K. Schum.) Katt.	E_subgibbosa_cla	29°–30° S	FK 27 (SGO) (Neotype), Región de Coquimbo, 30 km east of La Serena.
			Eggli and Leuenberger 3071 (CONC), Región de Coquimbo, 19 km west of La Serena.
			Eggli and Leuenberger 3079 (CONC), Región de Coquimbo, Quebrada Marquesa.
			HW 46 (CONC) [JF975695, JF975716], Región de Coquimbo, Las Rojas.
			HW 45 Región de Coquimbo, Cuesta San Antonio.
E. subgibbosa subsp. *nigrihorrida* (Backeb. ex A.W.Hill) Katt.	E_subgibbosa_nig	30°–31° S	FK 24 (SGO), Región de Coquimbo, Tongoy.
			FK 84 (SGO), Región de Coquimbo, Limarí river.
			FK 481 (SGO), Región de Coquimbo, Punta Teniente.
			FK 1095 (SGO), Región de Coquimbo, Limarí river.
			HW 628 (CONC) [JF975697, JF975718], Región de Coquimbo, El Teniente.
			HW 62, Región de Coquimbo, Cuesta las Cardas.
			HW 730, Región de Coquimbo, Quebrada Seca.

Table 1 continued

Species	Acronyms	Latitudinal distribution	Collection data
E. subgibbosa subsp. *vallenarensis* (F. Ritter) Katt.	E_subgibbosa_val	28° S	FK 79 (SGO) (Neotype), Región de Atacama, Maitencillo.
			HW 129 (CONC) [JF975699, JF975720], Región de Atacama, west of Vallenar.
E. subgibbosa subsp. *wagenknechtii* (F. Ritter) Katt.	E_subgibbosa_wag	29° S	FK 183 (SGO), Región de Coquimbo, Juan Soldado.
			FK 1091 (SGO), Región de Coquimbo, Juan Soldado.
			Eggli, Leuenberger and Arroyo-Leuenberger 2878 (CONC), Región de Coquimbo, Juan Soldado.
			HW 44 (CONC) [JF975700, JF975721], Región de Coquimbo, Chungungo.
			HW 358, Region de Atacama, Caleta Chañaral.
			HW 654, Región de Coquimbo, Cruz Grande.
E. villosa (Monv.) Katt.	E_villosa	28°–29° S	FK 71 (SGO) (Neotype), Región de Atacama, north of Huasco.
			FK 164 (SGO), Región de Atacama, Huayco (=Huasco).
			FK 467 (SGO), Región de Atacama, Sarco.
			FK 814 (SGO), Región de Atacama, Carrizal Bajo.
			FK 1028 (SGO), Región de Atacama, north of Huayco.
			Eggli and Leuenberger 2675 (CONC), Región de Coquimbo, Los Choros.
			Eggli and Leuenberger 2675 (CONC), Región de Coquimbo, El Trapiche.
			Eggli and Leuenberger 2967 (SGO), Región de Coquimbo, Los Choros.
			Eggli and Leuenberger 3001 (CONC), Región de Atacama, North of Huayco (=Huasco).
			HW 187 (CONC) [JF975702, JF975725], Región de Atacama, north of Huasco.
			HW 477, Región de Atacama, east of Llanos de Challe.
			HW 304, Región de Atacama, Aguadas Tongoy.
			HW 358, Región de Atacama, Caleta Chanaral.

The collection data included collector and collection number (HW for H.E. Walter and FK for F. Kattermann), region, and locality. Morphological data of the studied taxa were mainly taken from plants studied in the field (all HW collection numbers). Specimens from herbarium collections are identified in parentheses (CONC, Universidad de Concepción; SGO, Museo Nacional de Historia Natural), and when Genbank codes apply they also are given, in square brackets [trn*L*-trn*F*, rpl*32*-trn*L*]

units from subsection *Neoporteria* at species and infraspecific levels were chosen as an ingroup in all the phylogenetic analyses (recent taxonomic proposals of ingroups and outgroups are available in the electronic supplementary material, Appendix 1). Infraspecific taxa were included for two reasons: first, because of the problem of polymorphic character states within species (Nixon and Davis 1991), and second, because earlier studies suggested that some taxa previously classified at infraspecific levels might represent distinct species (Nyffeler and Eggli 1997; Walter 2008) or might belong to different groups (Walter 2008; Appendix 1, supplementary material). Several species from the Chilean subsections of *Eriosyce* sensu lato (subsection *Eriosyce*, subsection *Islaya*, subsection *Horridocactus* and subsection *Chileosyce*) were used as outgroups. In the morphological analysis we included eight outgroup species from *Eriosyce* sensu lato, four in the trn*L*-trn*F* and nine in the rpl*32*-trn*L* data set. We also included distantly related *Corryocactus brevistylus* (tribe Phyllocacteae subtribe Corryocactinae) in all analyses, and *Neowendermannia chilensis* in analyses that included rpl*32*-trn*L*. Voucher information and a complete list of the 21 *Eriosyce* sensu lato taxa with their collection data and the acronyms used in the analyses and their distribution are shown in Table 1.

Morphological dataset

The dataset consisted of 38 discrete multistate morphological characters. We decided to include eco-physiological characters because ex-habitat and seed-grown plants cultivated in the northern hemisphere had the same characters, suggesting a genetic background for those characters (Walter 2008). Thickness of epidermis and thickness of hypodermal layers are classified as discrete characters because both were adopted from Nyffeler and Eggli (1997). Discrete character states are shown in Table 2, and the resulting matrix is available in the electronic supplementary material (Appendix 2).

Molecular dataset

Fresh samples were frozen at −20°C and pulverized to a fine powder. Before DNA extraction, the tissue powder was suspended in HEPES buffer (pH 8.0) and centrifuged at 10,000 rpm for 5 min to remove mucilage (Setoguchi et al.

Table 2 Characters and character states for the cladistic analysis of *Neoporteria*

	Character	Character states				
1.	Root system	[0] fibrous	[1] intermediate	[2] taproot		
2.	Stem elongation	[0] columnar (>60 cm)	[1] subcolumnar (40–60 cm)	[2] globular to slightly elongate (5–40 cm)	[3] subglobular to flattened (<5 cm)	
3.	Stem color	[0] grey-green to reddish	[1] grass-green to yellowish green			
4.	Spine number	[0] 1–20	[1] 21–30	[2] 31–60		
5.	Central spines thickness	[0] thin acicular	[1] thick acicular	[2] thin hair-like	[3] not applicable	
6.	Central spines attitude	[0] straight to directed downwards	[1] straight radiant	[2] straight to recurved	[3] strongly contorted	[4] not applicable
7.	Radial spines attitude	[0] radiant	[1] curved upwards	[2] pectinate		
8.	Radial spines thickness	[0] majority thin acicular	[1] majority thick acicular	[2] thin hair-like		
9.	External perianth segments attitude	[0] straight	[1] curved downwards			
10.	Flower shape	[0] wide funnel-form	[1] funnel-form	[2] narrow funnel-form	[3] tubular	
11.	Ratio between the pericarpel length and the hypanthium length	[0] >0.70	[1] 0.50–0.70	[2] 0.35–0.49	[3] <0.35	
12.	Nectar chamber	[0] tubular	[1] basally widened, round	[2] basally widened, angular		
13.	Duration of individual anthesis	[0] 1–5 days	[1] 6–10 days	[2] >10 days		
14.	Total duration of anthesis	[0] 3–6 weeks	[1] 7–11 weeks	[2] 12–24 weeks		
15.	Main flowering period	[0] from end of winter to spring	[1] spring	[2] from autumn to late winter		
16.	Flowers and fruits simultaneous	[0] yes	[1] no			
17.	Style color	[0] whitish to yellowish	[1] whitish with upper third reddish	[2] red		
18.	Wool on tube and pericarpel	[0] short and scant	[1] dense			
19.	Tube and pericarpel bristles quantity	[0] many	[1] few	[2] absent		
20.	Fruit shape	[0] globular to subovoid	[1] ovoid	[2] clearly elongated		
21.	Seed testa surface	[0] smooth	[1] finely tuberculate	[2] ribbed		
22.	Central spines clearly differentiated from radials	[0] no	[1] yes	[2] not applicable		
23.	Inner perianth segments attitude	[0] directed outwards	[1] intermediate	[2] directed inwards		
24.	Scotonastic movement	[0] absent	[1] intermediate	[2] present		
25.	Flower size in relation to spine size	[0] flower < spines	[1] flower = spine	[2]flower > spines		
26.	Color of innermost perianth segments	[0] white or yellow	[1] bicolorous: inferior part whitish, superior fuchsia	[2] fuchsia	[3] red	
27.	Flower color	[0] never fuchsia	[1] fuchsia			
28.	Relief of epidermis	[0] flat	[1] bumpy	[2] short-papillate	[3] long-papillate	
29.	Thickness of epidermis layer (excluding bulging outer periclinal walls) (maxima)	[0] 20–30 μm	[1] 31–40 μm	[2] 41–70 μm		
30.	Secondary cell divisions of epidermis cells	[0] Only periclinal	[1] periclinal or oblique	[2] not applicable		

Table 2 continued

	Character	Character states			
31.	Number of periclinal and oblique secondary cell divisions in non-papillate cells	[0] none	[1] few	[2] many	[3] not applicable
32.	Number of periclinal and oblique secondary cell divisions in papillate cells	[0] none	[1] few	[2] many	[3] not applicable
33.	Number of cell layers in the hypodermis (maxima)	[0] 1–2	[1] 3	[2] 4–7	[3] not applicable
34.	Thickness of the hypodermis layer (maxima)	[0] 30–50 µm	[1] 60–110 µm	[2] 140–350 µm	[3] not applicable
35.	Firmness of the cortex tissue	[0] soft or very soft	[1] intermediate	[2] tough	
36.	Presence of mucilage in stem sections	[0] not mucilagious	[1] slightly or locally mucilaginous	[2] distinctly mucilaginous	[3] intensively mucilaginous
37.	Color of the central and inner cortex	[0] pale greenish or whitish	[1] intermediate	[2] green	[3] reddish
38.	Ratio of pith to plant diameter (in transverse sections at the widest diameter)	[0] 0.15–0.20	[1] 0.22–0.28	[2] 0.30–0.45	

Characters 28 to 38 and their states (apart from character state 37-3) were adopted from Nyffeler and Eggli (1997)

1998). Total genomic DNA was isolated using the CTAB procedure described by Doyle and Doyle (1987). Two genes were amplified using standard primers and procedures (rpl*32*-trn$L^{(UAG)}$: Shaw et al. 2007; trn*L*-trn*F*: Nyffeler 2002). When multibands were present in the gel, the bands corresponding to the size of the gene expected from the literature were cut out and cleaned using the Wizard® SV Gel and PCR clean-up system Promega kit (Qiagen). Fragments were amplified in 25-µL reactions (12.5 µL GoTaq colorless master (Promega, Madison, USA), 5.0 µL 10 mmol primer, 1.25 µL BSA, 0.0–3.0 µL 10 mmol MgCl, 4.25–6.25 µL ddH$_2$O) using an automated thermal cycler and standard PCR procedures, with PCR cycling time as follows: rpl*32*-trn*L*: denaturation at 80°C for 5 min followed by 45 cycles of denaturation at 95°C for 1 min, primer annealing at 48–56°C for 1 min, and primer extension at 65°C for 4 min; followed by a final extension step of 5 min at 65°C; trn*L*-trn*F*: denaturation at 94°C for 4 min, followed by 40 cycles of 94°C for 30 s, 46–54°C for 1 min, and 72°C for 90 s, and finished with a final elongation step at 72°C of 7 min. Sequencing was performed by Macrogen (Korea).

Sequences were edited using Mega 5.0 and aligned using Muscle first and then checked manually (Edgar 2004; Tamura et al. 2007), partitions were concatenated using Mesquite (Maddison and Maddison 2010) Taxon localities, the associated vouchers and the Genbank codes are listed in Table 1. Alignments are available from the corresponding author.

Phylogenetic analyses were conducted for each individual partition (morphology, rpl*32*-trn*L* and trn*L*-trn*F*) and for some partition combinations (rpl*32*-trn*L* + trn*L*-trn*F*, rpl*32*-trn*L* + trn*L*-trn*F* + morphology). Bayesian analyses were implemented using MrBayes version 3.1.2 (Huelsenbeck and Ronquist 2001) The best substitution model was GTR + G + I for each gene and was selected using the Akaike information criterion in MrModeltest version 2.0 (Nylander et al. 2004); in the case of morphology we utilized the standard unordered discrete evolution model. The best partitioning strategy between genes and between genes + morphology was realized using comparison of Bayes factors (Nylander et al. 2004), based on comparing the harmonic mean of the log-likelihoods of the post-burn-in trees from analyses. These analyses showed that the best partitioning strategy was the partition that included both genes (rpl*32*-trn*L* + trn*L*-trn*F*) and the partition that included both genes and morphology (rpl*32*-trn*L* + trn*L*-trn*F* + morphology). For each separate and combined analysis, we ran two replicate searches for 5×10^6 generations each, sampling every 1,000 generations and using default parameters.

In addition, tree searches using maximum likelihood analysis were conducted to genes partitions using RAxML version 7.0.3 (Stamatakis et al. 2008). This implementation of the likelihood method enables optimization of individual substitution models for different partitions. Thus, we applied the same combination of models (GTR + G + I) and partitioning strategies between and within genes as in the Bayesian analyses. Two hundred inferences were executed using RAxML on distinct randomized parsimony starting trees with 1,000 nonparametric bootstrap replicates.

Predictive distribution modeling and the geography of divergence

We used predictive distribution modeling (also known as climatic niche modeling) to infer taxa range extent associated to the spatial distribution of climatic suitability. We modeled the distribution of sister taxa using Maxent version 3.3.3e (Phillips et al. 2004, 2006). Two types of data are required to predict species ranges: environmental data and information on their known occurrence. The environmental layers consisted of the Bioclim climatic datasets which summarize temperature and precipitation dimensions in the environment (Hijmans et al. 2005). In spite of some criticisms (heterogeneous distribution of meteorological stations supplying data to construct the interpolated climatic models), Bioclim is the most complete climatic database available for Chile. With 19 layers and the appropriate formats for Geographic Information Systems, Bioclim has become widely used in evolutionary and biodiversity studies (Kozak and Wiens 2006; Raxworthy et al. 2007; Evans et al. 2009; Zizka et al. 2009).

Information on locality data was obtained from different sources: field excursions, literature and Chilean herbaria (CONC = Universidad de Concepción; SGO = Museo Nacional de Historia Natural). Cacti are not as well represented in herbaria as other families because of difficulties arising from drying and storing their tissues, but they have a long history of botanic and amateur work reflected in literature and in informal sources. To validate literature and herbaria localities, we verified the majority of the known populations in the field (Fig. 1). In this study, we included unpublished and new localities for most of the Chilean taxa. The number of localities per taxon ranged from four (*E. senilis* subsp. *coimasensis*) to 46 (*E. subgibbosa* var. *subgibbosa*). Maxent is considered the best model for managing datasets of small sample sizes, and its accuracy is proven to be greater for species with small geographic ranges and limited environmental tolerance as is the case in most *Neoporteria* taxa (Hernandez et al. 2006; Wisz et al. 2008).

Using Maxent, we calculated the average niche-based occurrence probabilities of 10 replicated models and we mapped probabilities >0.50 and >0.75. Overlapping was assessed by analyzing the probability of the co-occurrence of a pair of sister taxa obtained by multiplying their occurrence probabilities across their predicted distributions (for each pixel of 1 km^2 of the grids). The overlap percentage between both species was calculated by obtaining the area in which the probability of co-occurrence was >0.75 compared to the total range extent. Overlaps may vary between 0% (completely allopatric) and 100% (completely sympatric).

After running preliminary phylogenetic analyses we decided to add spatial evaluation of *E. chilensis*, since its floral morphology suggests an intermediate position between subsections *Neoporteria* and *Horridocactus*. As *E. chilensis* is restricted to a small area in which two *Neoporteria* taxa (*E. subgibbosa* var. *subgibbosa* and var. *litoralis*) and a species from subsection *Horridocactus* (*E. curvispina* (Bertero ex Colla) Katt. var. *mutabilis* (F.Ritter) Katt.) grow sympatrically, we checked if the overlap between the former species and each of the *Neoporteria* taxa matched the distribution range of *E. chilensis*.

Results

Phylogenetic relationships

The morphological data placed *E. islayensis* and *E. aurata* in a basal polytomy together with *Corryocatus brevistylus* (Fig. 2). All the *Neoporteria* sensu stricto taxa were included in a single well-supported clade that also comprised *E. taltalensis* (subsection *Horridocactus*) and *E. chilensis* in a basal position. The subclade comprising *E. odieri* and *E. krausii*, together with the rest of the subspecies of the *E. taltalensis* complex also received strong support. The sister pairs receiving strong support were *E. taltalensis/E. sociabilis, E. senilis* subsp. *senilis*/subsp. *coimasensis* and *E. subgibbosa* subsp. *clavata*/subsp. *nigrihorrida*, whereas the pair *E. subgibbosa* subsp. *subgibbosa*/subsp. *nigrihorida* received less support.

Bayesian and maximum likelihood analyses using single molecular markers revealed similar general phylogenetic relationships (Fig. 2), the basal species remained in the same position; in the rpl*32*-trn*L* partition that included *Neowerdermannia chilensis,* the latter was placed between *E. aurata* and *E. curvispina* subsp. *curvispina*. The most important difference between the trn*L*-trn*F* and rpl*32*-trn*L* analyses was the placement of *E. sociabilis* and *E. taltalensis* var. *taltalensis*: in the former analysis *E. taltalensis* and *E. sociabilis* were placed within the *Neoporteria* clade*,* whereas the latter placed it in the sister clade to *Neoporteria* sensu stricto compromising *E. odieri, E. krausii, E. paucicostata*, and the other taxa of the *E. taltalensis* complex. This difference might be explained by the fact that the rpl*32*-trn*L* partition included more taxa compared with the trn*L*-trn*F* partition.

The topologies of the trees resulting from analyses that combined all molecular data and molecular data plus morphology were almost identical, only some node supports changed. In both partitions *E. sociabilis* and *E. taltalensis* var. *taltalensis* were excluded from the *Neoporteria* clade (Fig. 3). Sister pairs that were strongly supported were *E. senilis* subsp. *senilis*/subsp. *coimasensis, E. subgibbosa* subsp. *clavata*/subsp. *nigrihorrida*, *E. subgibbosa* subsp. *subgibbosa*/subsp. *nigrihorrida*. As relationships among

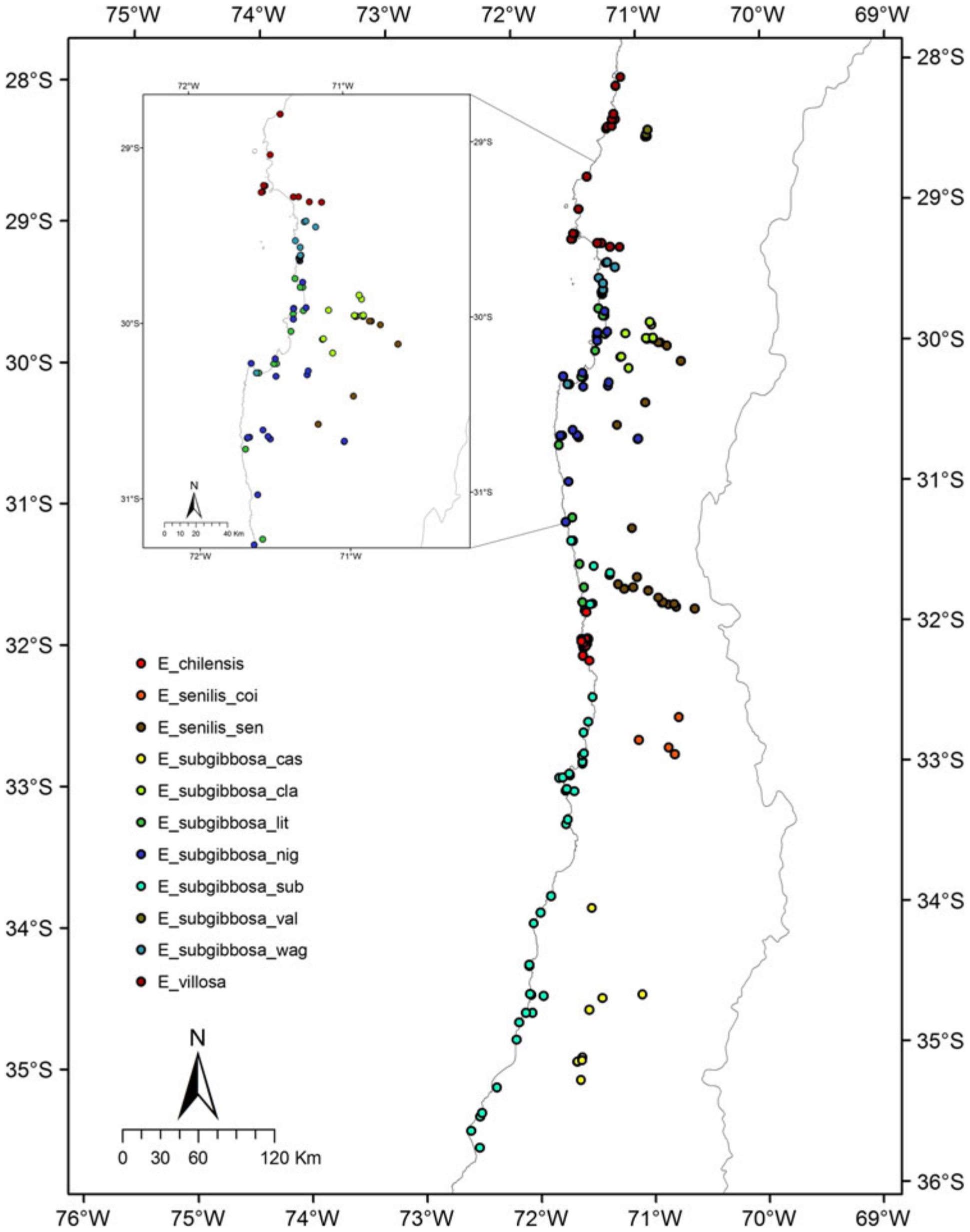


Fig. 1 Population localities of *Eriosyce* subgen. *Neoporteria* compiled from field excursions, literature and Chilean herbaria

E. villosa, *E. subgibbosa* subsp. *vallenarensis*/ *wagenknechtii* were poorly resolved in most analyses, we studied their distribution overlap.

Predictive distribution modeling and the geography of divergence

Predictive distribution modeling of species showed that the degree of geographic overlap between sister taxa is null (Fig. 4). All taxa showed <0.5 probabilities of co-occurrence between them, indicating an extensive allopatric distribution of relative taxa. *Eriosyce senilis* showed three disjunctions, one corresponding to subspecies *coimasensis*, the other two corresponding to the predicted areas of occurrence of *E. senilis* subsp. *senilis* that are separated by a large unsuitable intervening region (Fig. 4a). The sister pair *E. subgibbosa* subsp. *clavata*/*E. subgibbosa* subsp. *nigrihorrida* are distributed allopatrically, although the core area of their distributions ($P > 0.75$) is separated by a stretch of only 5 km (Fig. 4b). The group comprising *E. subgibbosa* subsp. *vallenarensis*, subsp. *wagenknechtii* and *E. villosa* showed a similar allopatric pattern (occurrence probabilities <0.5) (Fig. 4c). *E. subgibbosa* var. *subgibbosa* and var. *castanea* were shown to be separated by a distance of some 20 km (Fig. 4d).

In addition to that, predictive distribution modeling indicated that *E. subgibbosa* var. *litoralis* and *E. curvipina* var. *mutabilis* have null overlap between them, while the probability of an overlap of the latter species' distribution with *E. subgibbosa* var. *subgibbosa* was high (Fig. 5a). The

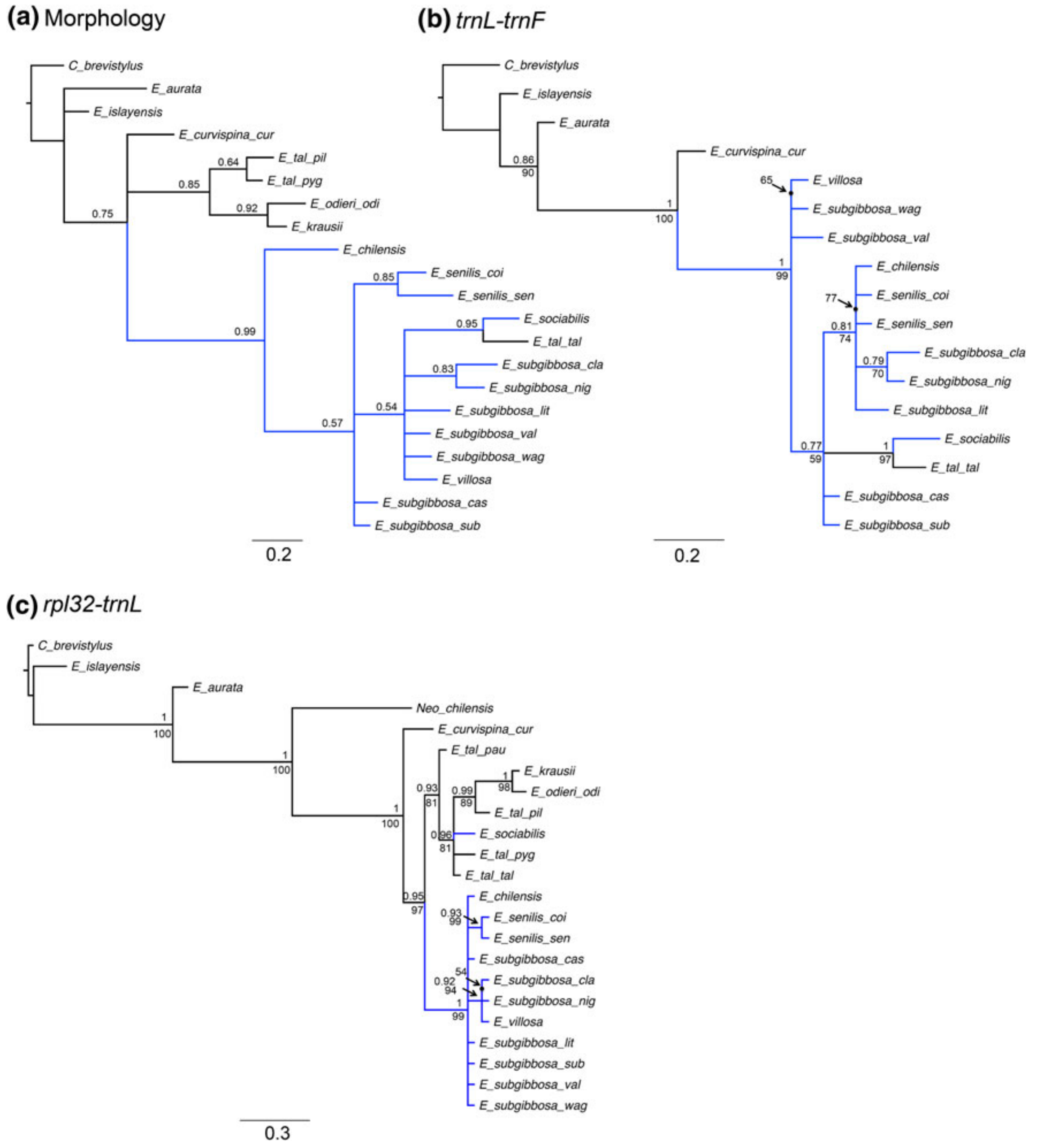


Fig. 2 Phylogeny of *Eriosyce* subgen. *Neoporteria* based on separate Bayesian analysis of morphology, and separate Bayesian and maximum likelihood analyses of molecular data based on trn*L*-trn*F* and rpl*32*-trn*L* (chloroplast DNA). *Numbers above branches* indicate a posteriori Bayesian support; *numbers below branches* indicate ML bootstrap support. *Filled black circles* indicate nodes that were supported with >50% of bootstrap support in ML analyses

overlap between these species matched 77.2% of the distribution extent of *E. chilensis* ($P > 0.75$; Fig. 5b).

Discussion

Phylogenetic relationships

The monophyly of *Neoporteria* sensu stricto has never been questioned seriously, as reflected by the fact that it was always seen as a distinct group, although at different taxonomic ranks (genus, subsection, subgroup, subgenus; supplementary material). When Kattermann (1994), however, broadened the concept of *Neoporteria* sensu stricto, proposing to place *E. chilensis* within subsection *Neoporteria,* some dispute arose, as the presentation of the case was contradictive: the cladogram (op. cit.) resulting from the phylogenetic analysis of *Eriosyce* sensu lato, did not place *E. chilensis* within the monophyletic subsection *Neoporteria,* but with subsection *Horridocactus* (Walter

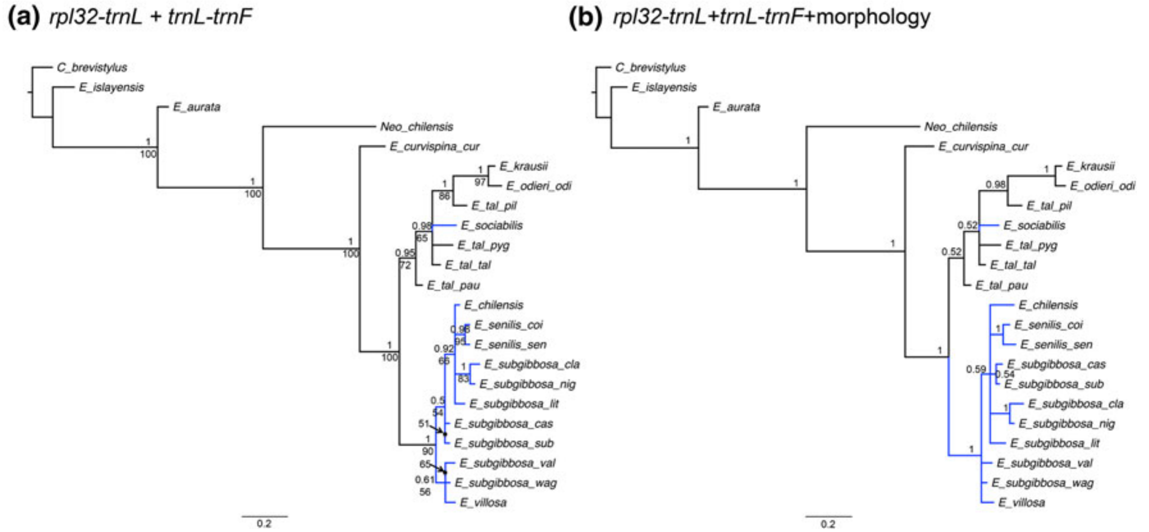


Fig. 3 Phylogeny of *Eriosyce* subgen. *Neoporteria* based on combined Bayesian and maximum likelihood analyses of molecular data: trn*L*-trn*F* + rpl*32*-trn*L* (chloroplast DNA), and combined Bayesian analysis of molecular and morphological data. *Numbers above branches* indicate a posteriori Bayesian support; *numbers below branches* indicate ML bootstrap support. *Filled black circles* indicate nodes that were supported with >50% of bootstrap support in ML analyses

2008). *E. chilensis*, an insect-pollinated species with wide funnel-form flowers, had before been considered a member of *Pyrrhocactus* (Ritter 1980; Hoffmann 1989; Zuloaga et al. 2008) or subgenus *Horridocactus* (Hoffmann and Walter 2004) for this reason. Kattermann (1994), however, placed it within subsection *Neoporteria*, arguing that the wide funnel-form flowers might indicate a reversal from hummingbird pollination to bee pollination. Nyffeler and Eggli's (1997) cladogram based on stem morphology and anatomical data suggested that *E. chilensis* is the most basal member of subsection *Neoporteria*.

The historical taxonomic complexity of the placement of *E. chilensis* either within *Horridocactus* /*Pyrrhocactus* or *Neoporteria* (Appendix 1) was reflected by our phylogenetic analyses, as different partitions of our dataset indicated two different positions of *E. chilensis* within the *Neoporteria* clade: in the analyses of combined molecular datasets *E. chilensis* was placed in the unresolved terminal subclade, whereas in the morphology-based tree it was placed basal to all ingroup taxa, most probably because of the various "pollination syndrome characters" in our morphological data set. This assumption coincides with Styles (1981), who reported that nearly all hummingbird flowers of North America have evolved from insect-pollinated species. On the other hand, in the analysis of Nyffeler and Eggli (1997), whose character set did not comprise any floral characters, it was also placed in a basal position within *Neoporteria*.

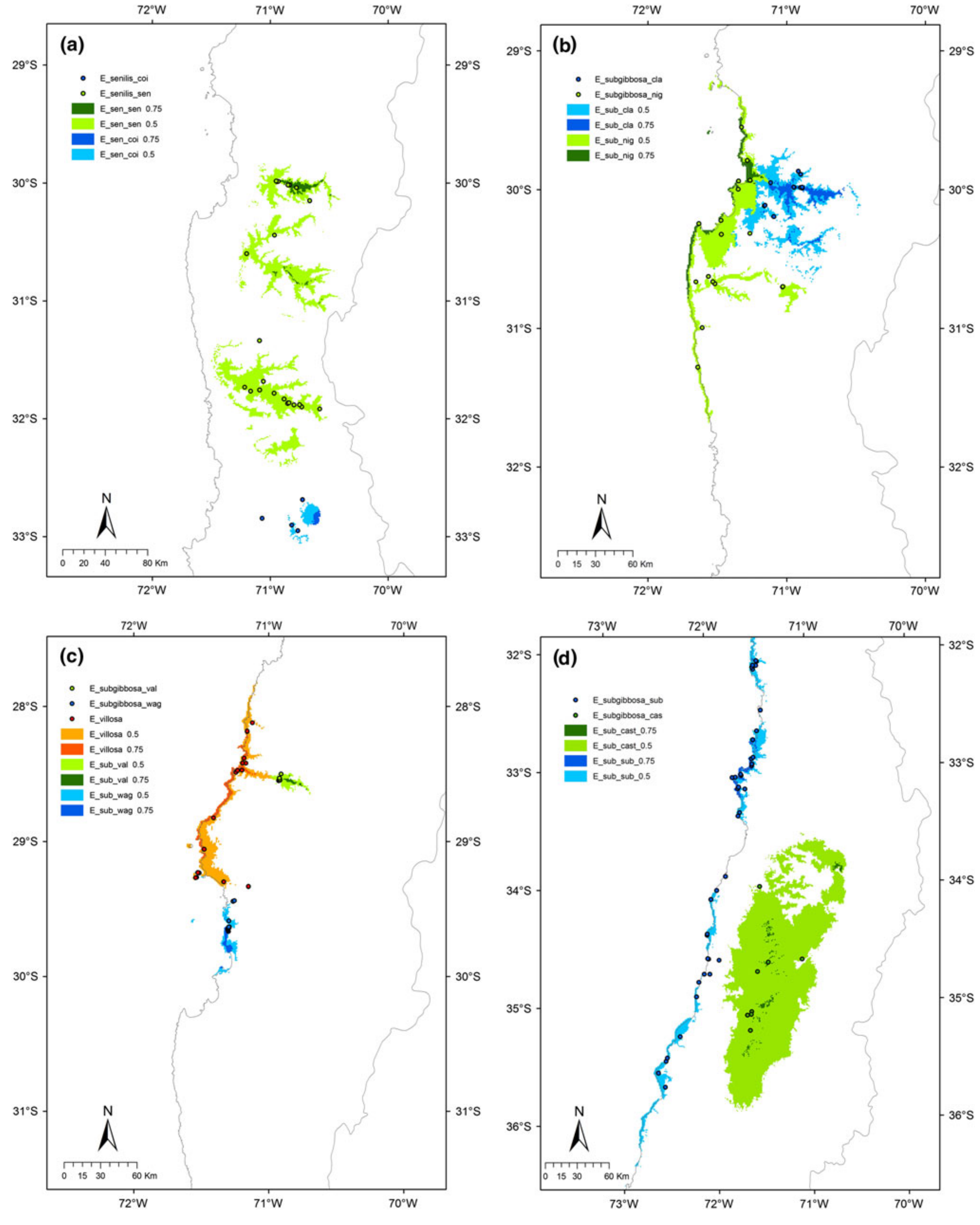
These contradictive results suggest that the morphology of *E. chilensis* may comprise several homoplasies, making it difficult to decide its phylogenetic placement. One plausible explanation for these homoplasies is that *E. chilensis* might share morphological traits between subsections *Neoporteria* and *Horridocactus*. Predictive distribution models showing the overlap of the possible parental species suggest that hybridization is plausible (see below).

Kattermann's (1994) broad concept of *E. subgibbosa*—including five heterotypic subspecies—was not corroborated by our analyses (morphological and molecular), because *E. subgibbosa* subsp. *subgibbosa* was never grouped in one clade. Our analysis based on the combined molecular markers (Fig. 3a) suggests the existence of at least three distinct entities within Kattermann's (1994) broad concept of *E. subgibbosa*:

1. *E. subgibbosa* var. *subgibbosa*/var *castanea*;
2. *E. subgibbosa* subsp. *nigrihorrida*/subsp. *clavata*; and
3. *E. subgibbosa* subsp. *wagenknechtii*/subsp. *vallenarensis* together with *E. villosa.*

This supports Walter's (2008) assumption that *E. subgibbosa* subsp. *wagenknechtii*/subsp. *vallenarensis* are much closer related to *E. villosa* than to *E. subgibbosa*.

Four different taxa were placed in the unresolved terminal subclade—*E. chilensis*, *E. senilis*, and *E. subgibbosa* subsp. *nigrihorrida*, subsp. *clavata* and var. *litoralis*—but, unexpectedly, our molecular data were not able to resolve the relationships between them. The exclusion of *E. subgibbosa* subsp. *clavata*, subsp. *nigrihorrida* and var. *litoralis* from the *E. subgibbosa* subsp. *subgibbosa* subclade, however, indicates that they might represent different species, a finding corroborating their classification by Walter (2008). A future study would probably have to


(a)
E_senilis_coi
E_senilis_sen
E_sen_sen 0.75
E_sen_sen 0.5
E_sen_coi 0.75
E_sen_coi 0.5
72°W
71°W
70°W
29°S
30°S
31°S
32°S
33°S
N
0 20 40 80 Km
(b)
E_subgibbosa_cla
E_subgibbosa_nig
E_sub_cla 0.5
E_sub_cla 0.75
E_sub_nig 0.5
E_sub_nig 0.75
72°W
71°W
70°W
29°S
30°S
31°S
32°S
N
0 15 30 60 Km
(c)
E_subgibbosa_val
E_subgibbosa_wag
E_villosa
E_villosa 0.5
E_villosa 0.75
E_sub_val 0.5
E_sub_val 0.75
E_sub_wag 0.5
E_sub_wag 0.75
72°W
71°W
70°W
28°S
29°S
30°S
31°S
N
0 15 30 60 Km
(d)
E_subgibbosa_sub
E_subgibbosa_cas
E_sub_cast_0.75
E_sub_cast_0.5
E_sub_sub_0.75
E_sub_sub_0.5
73°W
72°W
71°W
70°W
32°S
33°S
34°S
35°S
36°S
N
0 15 30 60 Km

◀ **Fig. 4** Predicted geographic distributions of selected sister taxa of *Eriosyce* subgen. *Neoporteria* based on ecological niche modeling. *Circles* are documented localities for each taxon. **a** *E. senilis* subsp. *senilis* and subsp. *coimasensis.* **b** *E. subgibbosa* subsp. *nigrihorrida* and *E. subgibbosa* subsp. *clavata*. **c** *E. subgibbosa* subsp. *vallenarensis*, subsp. *wagenknechtii* and *E. villosa.* **d** *E. subgibbosa* var. *subgibbosa* and var. *castanea*

sample inter and infra-populational variability to resolve relationships in this subclade.

The analyses based on the combined molecular (Fig. 3a) and molecular/morphological data (Fig. 3b) excluded *E. sociabilis* and *E. taltalensis* subsp. *taltalensis* from the *Neoporteria* clade, whereas our morphological and trn*L*-trn*F* (Fig. 2a, b) data included it in this clade. The cause of this inconsistency might be the less dense taxon sampling in the trn*L*-trn*F* partition compared with the rpl*32*-trn*L* partition. The gross morphologies of *E. sociabilis* and *E. taltalensis* subsp. *taltalensis* are strikingly similar (Ritter 1980; Walter 2008) and they share many flower characters, for example the fuchsia-red color, and the size or the narrow funnel-form hypanthia; the inner perianth segments of *E. sociabilis* are, however, erect to sometimes somewhat inclined inwards, one of the typical characters of a hummingbird syndrome. For these reasons, *E. sociabilis* has been considered a member of *Neoporteria* sensu stricto (a hummingbird-pollinated group) by all authors since Ritter (1963) described it as *Neoporteria sociabilis*. Our molecular data, however, placed *E. sociabilis* within the highly supported sister clade to *Neoporteria* comprising (amongst other taxa) the taxa of the *E. taltalensis* complex, thus suggesting that in the circumscription of Kattermann (1994), subsection *Neoporteria* is paraphyletic.

After Schlumpberger and Raguso (2008) had shown for a group of closely related species of *Echinopsis* that floral syndromes are particularly unreliable (Nyffeler and Eggli 2010), the exclusion of *E. sociabilis* from the *Neoporteria* clade by our molecular data seems to present another case documenting the fact that molecular analyses (Ritz et al. 2007) provide ample clarity that pollination syndromes are highly plastic and that there is convincing evidence that the same floral syndrome can evolve in parallel in the same clade (Nyffeler and Eggli 2010). It is noteworthy to mention that not only floral syndromes but also hummingbirds must be considered as “unreliable”, as they are not as

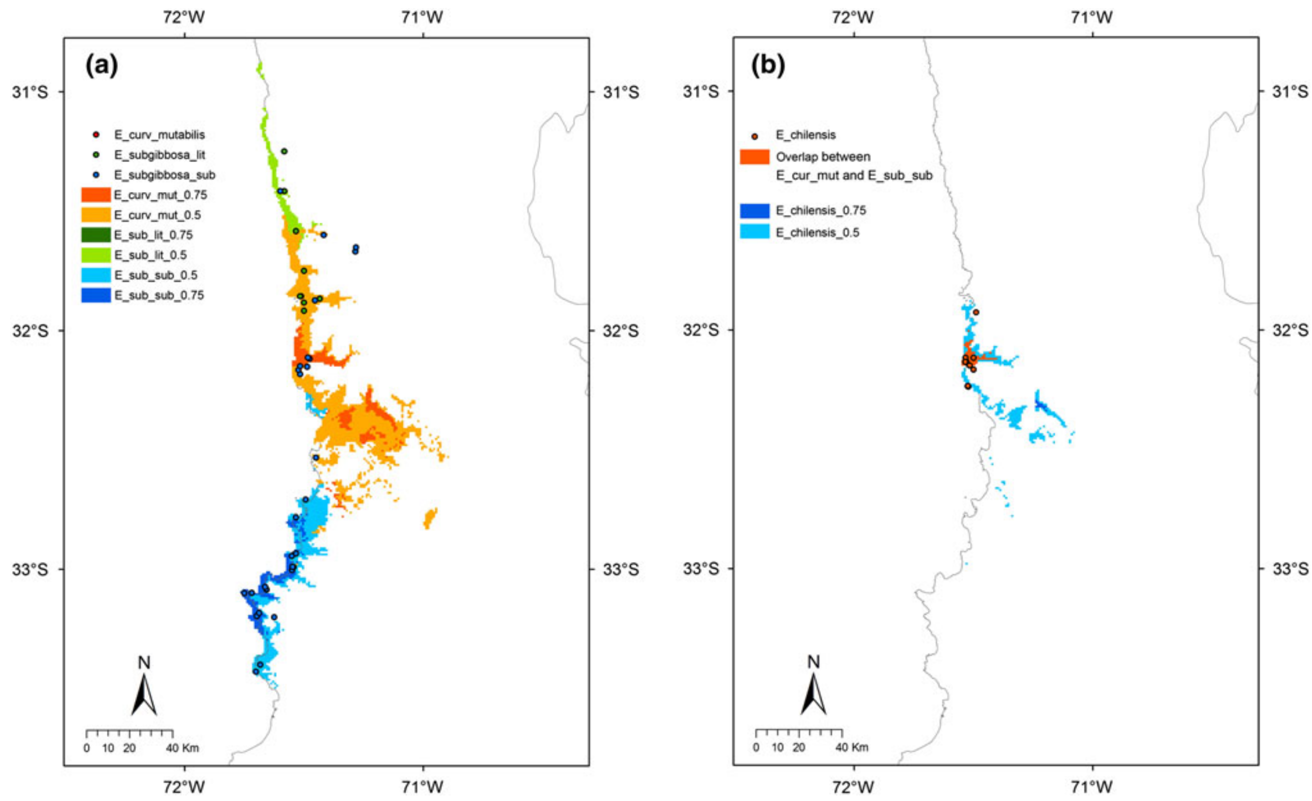


Fig. 5 Predicted geographic distributions of two subsections within *Eriosyce* whose distributions overlap in central coastal Chile. *Circles* are documented localities for each taxon. We evaluated the probability of co-occurrence of one *Horridocactus* and two *Neoporteria* taxa to determine if the estimated overlaps matched *E. chilensis* distribution. **a** Geographic distributions of *E. subgibbosa* var. *litoralis*/var. *subgibbosa* (subsect. *Neoporteria*) and *E. curvipina* var. *mutabilis* (subsect. *Horridocactus*). **b** overlap between *E. subgibbosa* var. *subgibbosa* and *E. curvispina* var. *mutabilis* and distribution of *E. chilensis*. We did not detect overlap with *E. subgibbosa* var. *litoralis*

specialized on "hummingbird flowers" as often suggested: they also might feed on non-tubular flowers with wide open corollas, for example those in *E. taltalensis* and *E. chilensis*—especially during the winter when, e.g., winter-blooming *E. taltalensis* subsp. *taltalensis* flowers are often the only flowers available (Walter 2008).

Predictive distribution modeling and the geography of divergence

Analyses of the degree of geographic overlap between sister taxa obtained from the cladistic analysis showed that most of the sister taxa are spatially segregated entities or have minimum overlap, suggesting that allopatric divergence is a widespread phenomenon in *Neoporteria* (Fig. 4). None of the sister taxa, (*E. subgibbosa* subsp. *clavata* / subsp. *nigrihorrida*; *E. subgibbosa* var. *subgibbosa*/ var. *castanea*; *E. subgibbosa* subsp. *wagenknechtii*/subsp. *vallenarensis*/ *E. villosa*; *E. senilis* subsp. *senilis*/ subsp. *coimasensis*) had any degree of predictable geographic overlap (Fig. 4).

Although it was not part of the objectives of this study to distinguish between the different types of allopatry, some particular aspects may be considered. Asymmetric range sizes between sister taxa have often been associated with peripatric speciation (Losos and Glor 2003); however, our sister taxa have similar range sizes (Fig. 4). This strongly suggests that their divergence originated from an allopatric vicariant event (probably because of climatic changes) and the low overlap may have been caused by recent and subtle changes in their distribution ranges (caused by climatic changes). Moreover, these taxa are located in the transitional zone between summer and winter rainfall, and the transitional zone between the hyper-arid and semi-arid ombrotypes of northern-central Chile which underwent continuous changes during the Holocene and Pleistocene (Latorre et al. 2002; Houston 2006; Luebert and Pliscoff 2006). During the Pleistocene, periods of glaciations created a series of wet–dry cycles, enabling the expansion of the range of the northernmost *Neoporteria* taxa during wet periods (Latorre et al. 2002; Maldonado et al. 2005), followed by a subsequent contraction of ranges, thus promoting population isolation during cycles of dry periods. During the Holocene, the climate became more arid (Maldonado et al. 2005), restricting the distribution of the northern *Neoporteria* taxa. Indeed, some of these populations might have survived in zones with oceanic fog dynamics (Cereceda et al. 2002, 2008), thus favoring long-term divergence between them. Other vicariant relict species from various plant families, for example *Griselinia* G.Forst. (Griseliniaceae), *Heliotropium* section *Cochranea* (Miers) Kuntze (Heliotropiaceae), *Moscharia* Ruiz et Pav. (Asteraceae) and *Tillandsia* L. (Bromeliaceae), are preserved in the northern fog oasis system. Although their separation had occurred in different geological eras, aridity had always contributed to their allopatric divergence (Dillon and Muñoz-Schick 1993; Katinas and Crisci 2000; Luebert and Wen 2008; Zizka et al. 2009; Guerrero et al. 2011).

The predicted spatial separation between *E. senilis* subsp. *senilis* / *E. senilis* subsp. *coimasensis* is approximately 50–100 km, suggesting that both taxa may belong to different evolutionary lineages and may even represent distinct species (Wiens 2004a). Interestingly, two spatially separated entities in *E. senilis* subsp. *senilis*, can be clearly distinguished from their predicted distributions: the populations between latitudes 30°–31° S (the Elqui and Limarí Valleys and adjacent regions) and the populations between 31°30′–32° S (Choapa Valley and adjacent regions). The extensive unsuitable intervening regions between these areas make gene flow between these populations unlikely. Yet, on the basis of their morphological similarity, they were seen as one taxonomic entity (i.e. *E. senilis* subsp. *senilis*) by Hoffmann and Walter (2004) and Hunt et al. (2006). In the past, some authors had considered the two populations as distinct taxa, classifying the northern populations as *E. senilis* subsp. *elquiensis* Katt., respectively *Neoporteria nidus* var. *gerocephala* (Y. Ito) Ritt., and the southern populations as *E. senilis* subsp. *senilis,* correspondingly *N. multicolor* F. Ritter (Ritter 1980; Kattermann 1994). Our spatial analysis supports Kattermann's and Ritter's division of this taxon into two taxonomic units. Less distance separates *E. subgibbosa* var. *subgibbosa* from *E. subgibbosa* var. *castanea* (~20 km) together with little morphological difference, suggesting that climatic barriers and the resulting reproductive isolation were imposed more recently and thus the divergence between the two taxa is still in an early stage.

Predictive distribution models showed that the overlap between *E. subgibbosa* var. *subgibbosa* and *E. curvispina* var. *mutabilis* matches with a high percentage of the distribution of *E. chilensis*, suggesting that both might be parental species of *E. chilensis.* However, phylogenetic analyses placed *E. chilensis* with *E. subgibbosa* var. *litoralis* suggesting genetic proximity and a complex scenario of species reproductive interactions. Further study is needed to test *E. chilensis'* reticular origin, and extensive genetic sampling at the population level and detailed evaluations of the reproductive biology of the four species.

Predictive distribution modeling and the phylogenetic analyses indicate that most of our taxonomic units correspond to divergent evolutionary lineages with different temporal stages of speciation and suggest that these lineages mostly originated as a result of historical vicariant events that resulted in the splitting of one common ancestor into two new taxa. The role of pollinators in driving speciation seems to be less important than geographic isolation caused by climatic tolerances, although, less frequently, pollinator guilds and the phenology of species might be important in reticular speciation.

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