BIOGEOGRAFÍA Y EVOLUCIÓN DE LA FAMILIA *CACTACEAE*: DIVERGENCIA DEL GRUPO *ERIOSYCE* SUBGEN. *NEOPORTERIA* BAJO GRADIENTES CLIMÁTICOS EN CHILE MEDITERRÁNEO.

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Por

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Dedicado a:

A mi hijo Dante

Eriosyce subgibbosa var. *litoralis,* Quebrada El Teniente, Región de Coquimbo, Chile

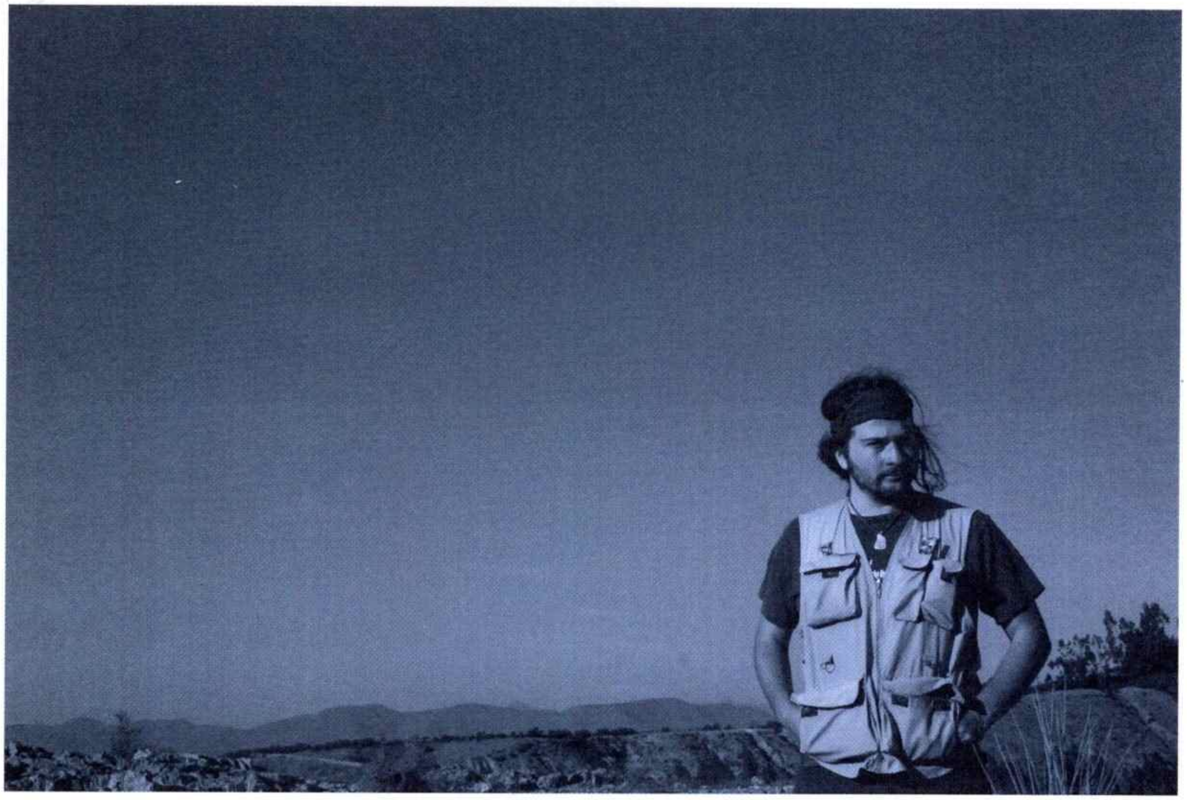
*

Tù, cactus de las arenas,
pequeño bruto inmóvil,
solitario,
tú fuiste el elegido
y pronto
antes de que otra flor te
desafiara
los botones
de sangre
de tus sagrados dedos
se hicieron flor rosada,
pétalos milagrosos.

*

Fragmento de 'Oda al Cactus de la Costa'
Pablo Neruda
\- Nuevas odas elementales (1955) -

RESEÑA



Pablo C. Guerrero Martin

(Santiago de Chile, 1979)

Biólogo mención en Medio Ambiente, nació en Santiago donde ha realizado toda su formación académica. Es Bachiller en Ciencias Naturales y Exactas (1998), Licenciado en Ciencias Ambientales (2001) y Magíster en Ciencias Biológicas (2005), todos los grados obtenidos en la Universidad de Chile. Entre los años 2004-2007 fue investigador del Programa Nacional de Recursos Fitogenéticos del Instituto de Investigaciones Agropecuarias (INIA), desempañado sus funciones en el Banco de Semillas ubicado en Vicuña, Región de Coquimbo. Adicionalmente ha sido profesor principal del curso de Sistemática y Taxonomía Vegetal de la Universidad Central de Chile. Actualmente se encuentra vinculado al Instituto de Ecología y Biodiversidad (IEB) en la Universidad de Chile. Dentro de la investigación que ha desarrollado destaca el interés por la conservación de la biodiversidad y la evolución de la flora de origen subtropical.

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CAPÍTULO I: INTRODUCCIÓN GENERAL

I.1 ANTECEDENTES

Un aspecto central en ecología, biogeografía y biología evolutiva son los mecanismos que determinan el origen de las especies y de la diversidad biológica en su conjunto (Brown y Lomolino 1998; Coyne y Orr 2004; Futuyma 2009). En este sentido, el nicho ecológico es un concepto transversal, particularmente cuando se estudian los componentes del nicho en relación a las condiciones ambientales requeridas para que las especies puedan vivir y reproducirse (e.g. nicho de "Grinnell": Grinnell 1917; Soberón 2007; Colwell y Rangel 2009). La robustez de esta relación se encuentra sustentada en que el clima es fundamental en dar forma a patrones de riqueza al incidir en la diversificación y / o extinción de especies (Willig *et al.* 2003; Rahbek *et al.* 2007; Wiens 2011), aislamiento geográfico (Raxworthy *et al.* 2007; Wiens 2004b) y de cambios en el nicho ecológico (Pearman *et al.* 2008). La covariación de un gradiente geográfico (e.g. latitud, batimetría, altitud) y la riqueza de especies sugiere la existencia de una asociación de ambos patrones a través del mecanismo de diversificación de ese grupo, es decir que existe una asociación entre las tolerancias climáticas de las especies con las variables atmosféricas incluidas en el gradiente geográfico. En un escenario en que los gradientes de precipitaciones o temperatura inciden sobre los patrones de distribución, se espera una disminución de la riqueza y un aumento del rango de geográfico de las especies hacia los polos y las cumbres de montañas (Rapoport 1979; Stevens 1989; 1992; Willig *et al.* 2003). En ese sentido, si la riqueza de especies disminuye con la elevación, es plausible pensar que los factores climáticos que covarían con la elevación imponen restricciones ecológicamente relevantes para las especies de ese grupo (Stevens 1992).

El nicho ecológico abordado como una propiedad dinámica de un clado es una mirada que permite estudiar los cambios de los requerimientos de las especies en el tiempo evolutivo, y sus efectos en la generación de otros patrones (Losos 2008; Pearman *et al.* 2008; Wiens *et al.* 2010). Una visión clásica de esta dinámica, indica que por medio de la selección natural podría producirse divergencia en los nichos ecológicos entre linajes que habitan de manera simpátrida (Mayr 1947). El mecanismo invocado para este cambio del nicho es la reducción en el co-uso de recursos por los individuos de una población en expansión numérica (Hutchinson 1957; 1959; MacArthur y Levins 1964), o adaptación local a condiciones climáticas diferenciales (Stebbins 1952; Axelrod 1967). Si la separación de los individuos en los ejes del nicho es lo suficientemente importante, se puede producir aislamiento reproductivo entre los individuos (Lack 1940; Mayr 1947).

En las últimas dos décadas, existen crecientes evidencias de que muchos linajes tenderían a mantener sus nichos ecológicos invariantes, incluso mucho después de que ha ocurrido especiación (Peterson *et al.* 2001; Prinzing *et al.* 2001; 2002; Wiens y Graham 2005; Pearman *et al.* 2008; Wiens *et al.* 2010). Este fenómeno se denomina conservatismo o estasis de nicho y podría estar relacionado de manera estrecha con el proceso de especiación alopátrida, particularmente en regiones con cambios climáticos (Wiens 2004a; Kosak y Wiens 2007). El conservatismo de nicho implica que las condiciones ecológicas apropiadas para los individuos se mantienen constantes en el tiempo, aún cuando puedan existir cambios climáticos. En ese sentido bajo cambios climáticos las especies al no poder adaptarse a las nuevas condiciones, deben seguir el corrimiento de la configuración climática apropiada (dentro del nicho) en la medida que se desplaza en un gradiente geográfico (Wiens 2004a). Restricciones a la dispersión o cambios climáticos rápidos pueden llevar a la extinción local y global de una especie (Wiens y Graham 2005).

La evolución de la familia Cactaceae ha sido de gran interés dentro de la biología evolutiva de plantas debido a que es una familia altamente diversificada con cuatro subfamilias, cerca de 100 géneros y 1500 especies, siendo una de las familias de angiospermas más conspicuas y diversas de las zonas áridas de América (Hershkovitz y Zimmer 1997; Hunt *et al.* 2006). Debido a su elevada diversidad, las cactáceas posibilitan los estudio cuantitativos asociados a la riqueza y diversificación, particularmente en zonas áridas y semiáridas del Neotrópico. Dentro de la enorme diversidad de cactáceas, existen numerosas especies que se encuentran en baja abundancia y que poseen distribución restringida. Sin embargo, otras especies son abundantes y se encuentran ampliamente distribuidas en el espacio, ocupando vastas zonas geográficas. Dentro de esta gama de posibilidades, existen reportes en cactáceas acerca de una asociación entre riqueza de especies y rango geográfico con la latitud (Mourelle y Ezcurra 1997a).

Chile es un país diverso en cactáceas con al menos 90 especies, 17 géneros y representantes de las cuatro subfamilias (Hoffmann y Walter 2004; Ortega-Baes y Godínez-Alvarez 2006) (Fig. 1). Sin embargo, ha existido un histórico déficit de estudios de esta familia en comparación con otros países como México, Brasil y Argentina. Además, el Desierto de Atacama y el mediterráneo centro de Chile configuran condiciones geográficas excepcionales para evaluar la diversificación y mecanismos de divergencia en relación a gradientes climáticos y geográficos. Por ejemplo, entre los 20° y 37° de latitud sur existe un importante gradiente climático caracterizado por la casi ausencia de precipitaciones en el norte hasta zonas con más de 1.000 mm de precipitaciones anuales en el sur (Luebert y Pliscoff 2006). Conjuntamente existe un gradiente altitudinal asociado, la variación longitudinal es menor a otros gradientes climáticos como en norte América y Asia (reduciendo el efecto área), y finalmente, la biodiversidad es altamente endémica producto de una historia evolutiva en común.

El género *Eriosyce sensu lato* (Kattermann 1994) es un gran género sudamericano de la tribu *Notocactaceae* (Cactaceae), incluye al menos 30 especies y constituye el grupo de cactáceas más diverso de Chile (Kattermann 1994, Anderson 2001, Hoffmann y Walter 2004, Hunt *et al.* 2006). Dentro de *Eriosyce sensu lato* se encuentran varios subgrupos: *Eriosyce sensu stricto* (endémico de Chile), *Pyrrhocactus* (endémico de Argentina), *Islaya* (distribuido en

Chile y Perú), *Neoporteria* (endémico de Chile), *Horridocactus* (endémico de Chile) y *Chileosyce* (endémico de Chile). *Eriosyce* subgénero *Neoporteria* (*Neoporteria*, de ahora en adelante), es un grupo conocido por sus flores con tépalos de color fuchsia y y centro blanco (Fig 2) (Walter 2008). El género fue descrito por primera vez en 1922 por Britton y Rose usando como tipo a *Echinocactus subgibbosus* Haw. [= *Eriosyce subgibbosa* (Haw.) Katt] espécimen colectado en los alrededores de Valparaíso (Fig. 3). *Neoporteria* es uno de los grupos más diversos de *Eriosyce* al tener unas 11 taxa endémicas distribuidas principalmente en el litoral desde el norte de Huasco hasta Concepción (28° S - 36° S) (Fig. 4). La gran distribución de este grupo en Chile central incluye diferentes condiciones macro-climáticas (Luebert y Pliscoff 2006). La gran diversificación de *Neoporteria* y su distribución en Chile central hacen de este grupo un buen sistema para estudiar las consecuencias de cambios climáticos sobre el proceso de especiación. Sin embargo, se desconocen hasta ahora las relaciones filogenéticas del grupo, dificultando la realización de análisis biogeográficos y macro-evolutivos.

En esta tesis se evaluaron patrones biogeográficos (riqueza y rango geográfico) de las cactáceas endémicas del Desierto de Atacama y Chile mediterráneo en relación a gradientes geográficos (elevación y altitud) y climáticos (precipitaciones y temperatura). Adicionalmente, se estableció una hipótesis filogenética para *Neoporteria,* basada en caracteres moleculares para estudiar la dinámica de nicho climático a lo largo de tiempo evolutivo. Para evaluar la relación de cambios climáticos y la dinámica filogenética de nicho en la divergencia de *Neoporteria*, se realizaron comparaciones entre la configuración climática del nicho de taxa hermanas. Finalmente, se evaluó el nicho fundamental de la germinación, mediante experimentos de jardín común con el objetivo de comparar ese dominio del nicho respecto al nicho climático.

I. 2 HIPÓTESIS Y OBJETIVOS

HIPOTESIS GENERAL

1.- Si los gradientes de temperatura y precipitaciones existentes en el Desierto de Atacama y Chile mediterráneo han constituido una restricción significativa y gradual para la sobrevivencia de especies de cactáceas, entonces la riqueza de especies debiera disminuir y los rangos de distribución debieran aumentar en relación al incremento de la latitud y altitud.

2.- Si los cambios climáticos históricos han inducido la diversificación del grupo *Neoporteria* a través de la intensificación de los gradientes de temperatura y precipitaciones, entonces el nicho climático de las taxa debiera evolucionar y ese cambio debe inducir la separación geográfica de taxa hermanas.

OBJETIVOS

(i) Evaluar la relación de los gradientes geográficos (latitud y altitud) en los patrones de riqueza y rango geográfico de las cactáceas endémicas al Desierto de Atacama y Chile mediterráneo.

(ii) Estimar el patrón de distribución geográfica de grupos de taxa hermanas de *Neoporteria* considerando las relaciones filogenéticas del grupo.

(iii) Inferir las consecuencias de la dinámica de nicho en la divergencia entre taxa hermanas dentro del grupo *Neoporteria* (Cactaceae).

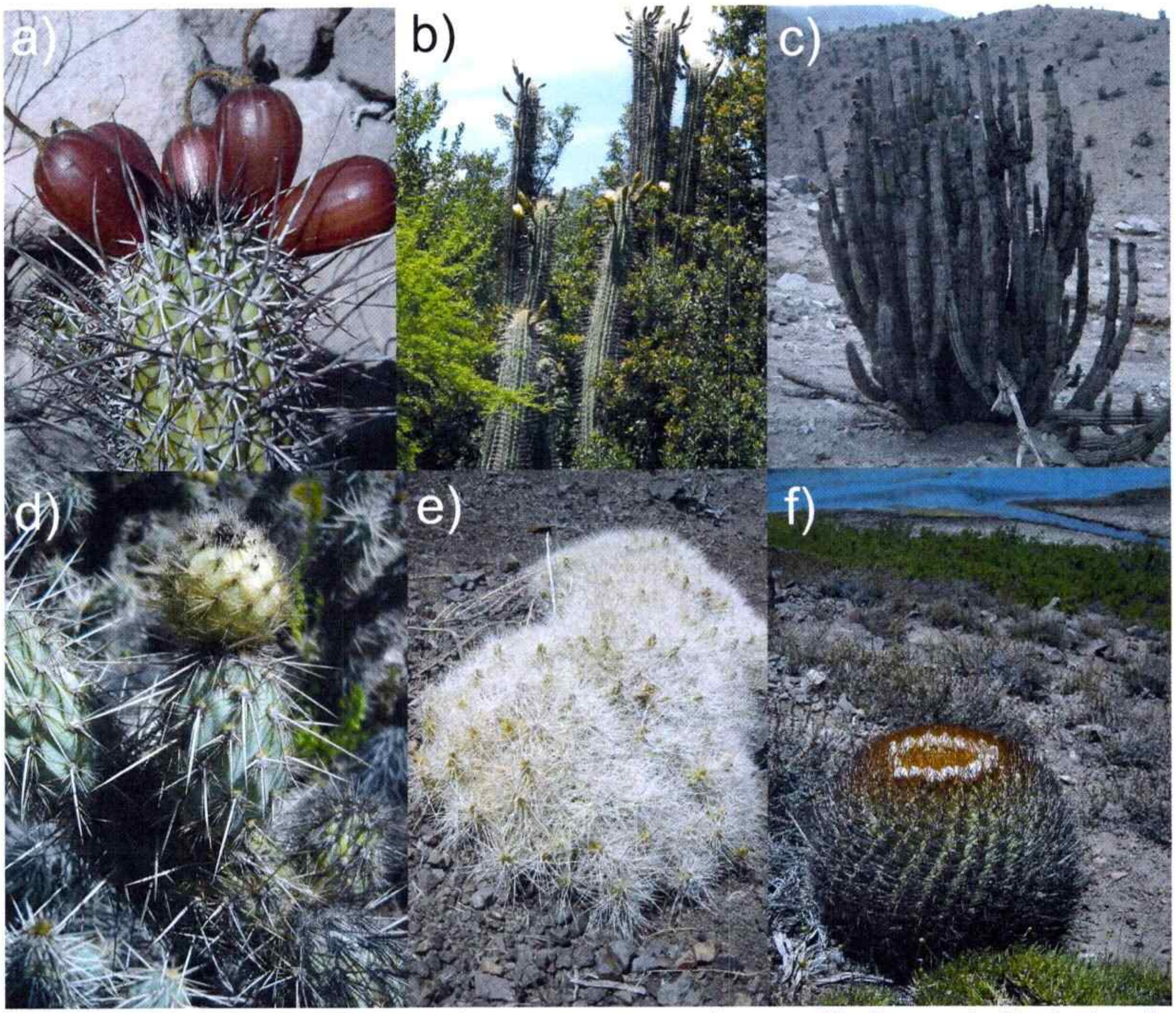


Figura I.1. Géneros de cactáceas con especies endémicas al Desierto de Atacama y Chile mediterráneo. a) *Haageocereus fascicularis* (Región de Arica y Parinacota), b) *Echinopsis* (= *Trichocereus*) *chiloensis* (Región Metropolitana), c) *Eulychnia iquiquensis* (Región de Antofagasta), d) *Miqueliopuntia miquelii* (Región de Atacama), e) *Maihueniopsis grandiflora* (Región de Coquimbo), y f) *Eriosyce aurata* (Región de Valparaíso). [Fotografías del autor].

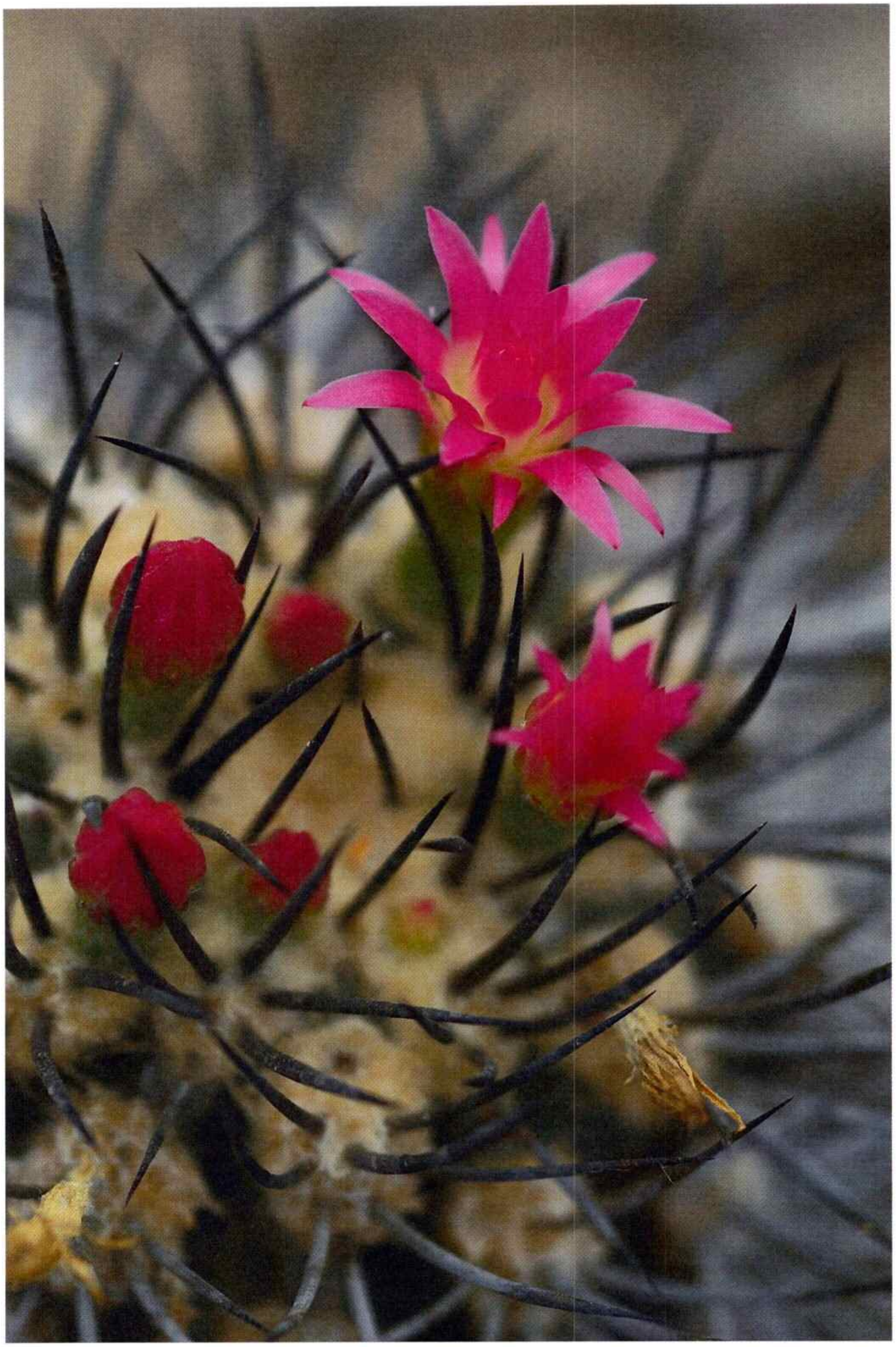
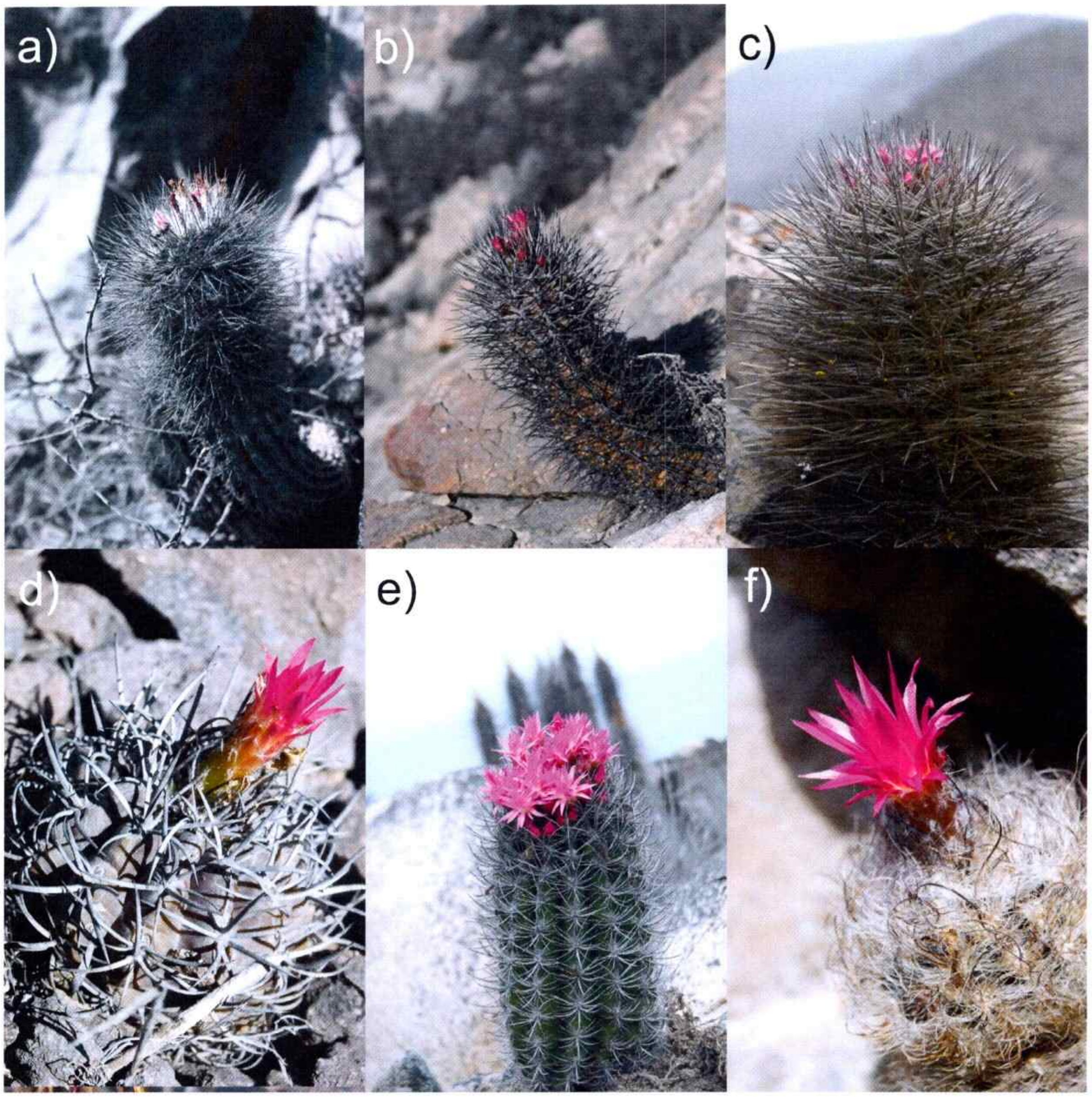


Figura I.2 Flor y botones florales de *Eriosyce subgibbosa* subsp. *nigrihorrida,* se observa la bicoloración fuschsia y blanco de las flores característica compartida del grupo *Neoporteria sensu stricto.*

Figura I.3 Especímen de *Eriosyce subgibbosa* en plena floración durante el mes de octubre (sur de Valparaíso). Esta fue la especie "tipo" utilizada por Britton y Rose (1922) para describir el género *Neoporteria* dedicado al entomógo Carlos Porter. La ilustración (abajo) corresponde a aquella utilizada originalmente por Britton y Rose.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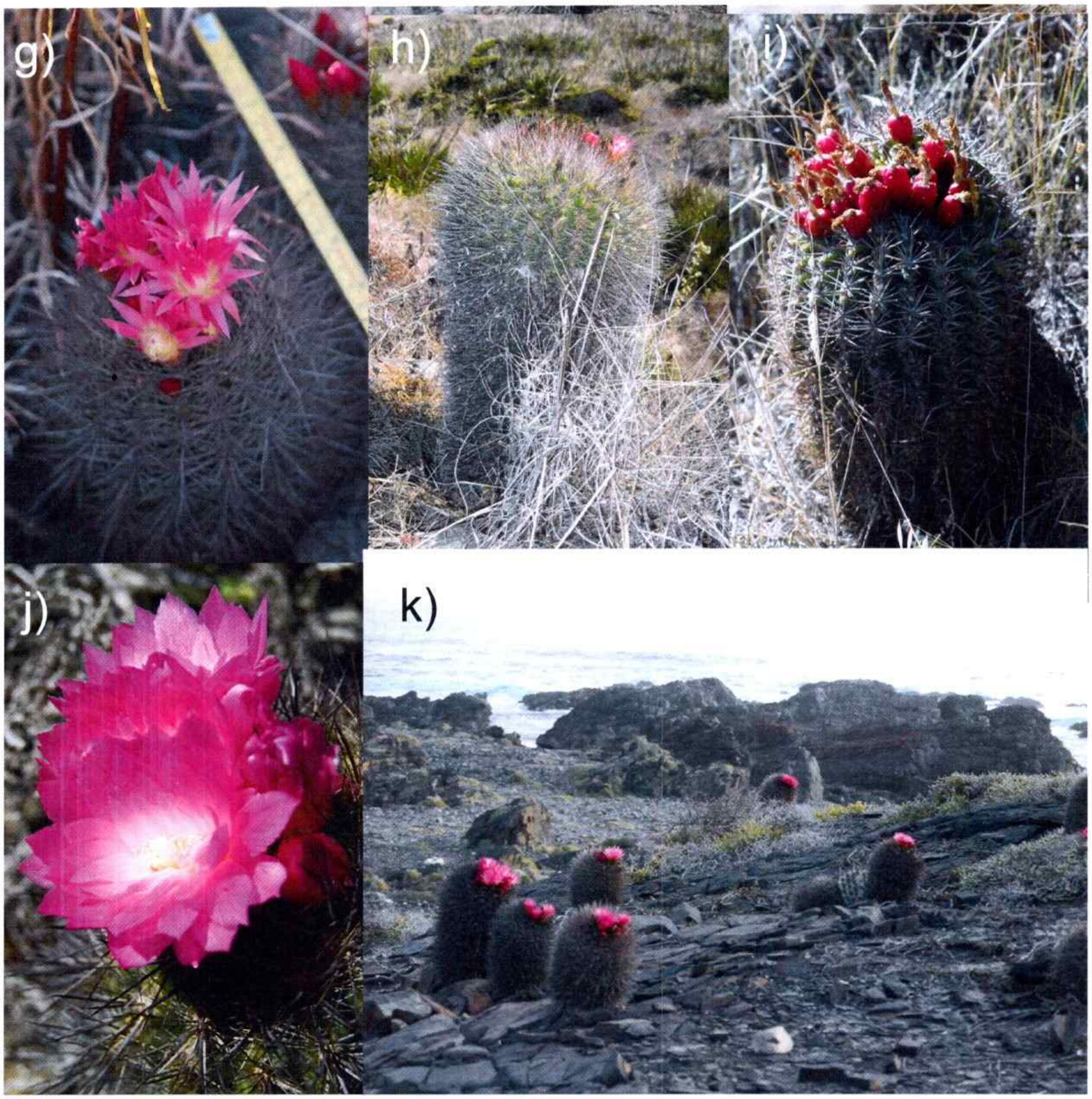

Figura I.4 Diversidad taxonómica del clado *Eriosyce* subgen. *Neoporteria*: a) *E. villosa*, b) *E. subgibbosa* subsp. *vallenarensis*, c) *E. subgibbosa* subsp. *wagenknechtii*, d) *E. subgibbosa* subsp. *clavata*, e) *E. subgibbosa* subsp. *nigrihorrida*, f) *E. senilis* subsp. *senilis*, g) *E. senilis* subsp. *coimasensis*, h) *E. subgibbosa* var. *subgibbosa*, i) *E. subgibbosa* var. *castanea*, j) *E. chilensis*, k) *E. subgibbosa* var. *litoralis*. [Fotografías del autor excepto "g" e "i" de M. Rosas].

Guerrero P.C., Durán A.P. and H.E. Walter. 2011.
Journal of Arid Environments 75: 991-997

CHAPTER II: LATITUDINAL AND ALTITUDINAL PATTERNS OF THE ENDEMIC CACTI FROM THE ATACAMA DESERT TO MEDITERRANEAN CHILE

II.1 ABSTRACT

In this study we describe the biogeographic patterns of the endemic cacti from the Atacama Desert to the Mediterranean area of Chile. Our goals were: (1) to identify areas of high endemism, (2) to test Rapoport's rule, (3) to test the geometric constraints hypothesis, (4) to explore temperature and precipitation as explanatory variables of species richness. We used a list of 72 species of cacti, ranging from 18° to 36° S and from 0 to 4,500 masl. A Bayesian analysis of Endemicity (BAE) was used to evaluate hierarchical relationships of endemism between different latitudinal bands. Rapoport's rule was evaluated by examining the relationships between latitudinal/altitudinal mid-point, latitudinal/altitudinal range extent and species richness. The geometric constraints hypothesis was tested by examining the existence of mid-domain effect. The BAE indicated two areas of endemism: (1) the northern area between 18° S and 26° S, and (2) the southern area between 27° S and 36° S. The shape of the latitudinal gradient is non-linear, supporting the geometric constraints hypothesis. Altitudinal patterns, however, support Rapoport's rule; a peak of endemism was found at low altitudes. The explanatory variables were elevation, minimum temperature of the coldest month, mean temperature of wettest quarter and annual precipitation.

KEY WORDS: Cactaceae; Rapoport's rule; geometric constraints; Bayesian analysis; climatic control

II.2. INTRODUCTION

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

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

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

The relation of species richness gradients and endemic richness is critical to our understanding of the diversification of specious groups (such as Cactaceae). Species richness and endemism are expected to be coupled when they are shaped by the same isolation mechanisms (Vetaas and Grytnes 2002). The endemism and species richness of Chilean cacti is one of the highest in the

Chilean angiosperm families (Marticorena 1990; Hoffman and Walter 2004; Hunt *et al.* 2006). All endemic cacti are exclusively distributed between 18° S and 36° S within the Chilean portion of the Arid Diagonal, suggesting that environmental gradients and hard geographic boundaries affect endemism patterns.

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

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

II.2. MATERIAL AND METHODS

Taxonomic database

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

Bayesian analysis of Endemicity (BAE)

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

In the BMCMC, the Bayesian statistical procedure uses the empirical data (observations) to update a prior probability distribution to a posterior probability distribution (Ronquist 2004). Posterior probability distributions are sampled by a Markov chain Monte Carlo method in order to obtain a stationary and most credible condition (see Ronquist 2004 for details). Likelihood values and hypotheses of area relationships were generated using the M2P model with no reversible time (directional) implemented in the software BayesPhylogenies (Pagel and Meade 2004). The M2P runs with presence/absence data with a non-time-reversible (i.e. directional) model, allowing the rates of change from 0 to 1 to differ from the rate of change from 1 to 0 (see BayesPhylogenies Manual p. 5). In our study this corresponds to the number of species gained along lineages (i.e. branches of the tree) resulting from ecological processes of immigration and/or an evolutionary process of speciation. Approximately 9,000 trees were generated using the BMCMC procedure, sampling every 1,000th tree to assure that successive samples were independent. We graphically detected the convergence zone of the Markov Chain by plotting trees and their likelihood values, and then removing all trees sampled before the convergence zone (Pagel and Meade 2004).

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

We characterized the latitudinal patterns of species richness and distribution ranges of species based on a binary presence/absence matrix. The sum of elements along a row (i.e., latitudinal bands where the species is present) is the distributional range of a species, and the sum of elements along a column (i.e., number of species within this latitudinal band) is the species richness in that latitudinal band. In this analysis, by species richness we mean the number of species occurring in a latitudinal band. Also, we characterized the altitudinal patterns of species richness and distribution ranges of species by constructing an altitudinal presence/absence matrix ranging from 0 to 4,500 m.a.s.l. Again, rows represent species, but in this matrix columns are altitudinal bands of 250-m. Therefore, the sum of elements along a row is the distribution range of a species, and the sum of elements along a column is the species richness in that altitudinal band. By species richness we mean the number of species.

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

Climatic drivers of species richness

In addition to the evaluation of latitudinal/altitudinal patterns, we studied the underlying relationship between species richness and climatic variables utilizing a latitude/longitude grid. In this analysis we wanted to reduce spatial autocorrelation to detect the influence of climate and elevation in determining variation in richness. We selected some Bioclim variables from the WORLDCLIM dataset (Hijmans *et al.* 2005) by choosing one of a group of highly correlated variables. The employed variables were: annual mean temperature (Bio1), mean diurnal temperature range (mean of monthly [maximum temperature - minimum temperature]) (Bio2), isothermality (Bio3), minimum temperature of the coldest month (bio6), annual temperature range (Bio7), mean temperature of wettest quarter (Bio8), annual precipitation (Bio12), precipitation seasonality (Bio15) and precipitation of warmest quarter (Bio18). We computed simultaneous autoregressive (SAR) models to estimate regression coefficients while accounting for spatial autocorrelation of each of the climatic variables together with the interaction of annual mean temperature and annual precipitation (Tognelli and Kelt 2004; Rahbek *et al.* 2007; Rangel *et al.* 2010). In this analysis, by species richness we mean the number of species occurring in a cell of the 0.5° x 0.5° map, which approximates species density (Gotelli and Colwell 2001; Rahbek *et al.* 2007).

II.3 RESULTS

Bayesian Analysis of Endemicity

The BAE showed two highly supported large areas of endemism: (1) the northern area between 18° S and 26° S, and (2) the southern area between 27° S and 36 °S (Fig. 1). The longitude of the phylogram branches showed that within both areas endemism was highest in north-central Chile and gradually decreased towards the extreme north and south (Fig. 1). The northern area showed the highest level of endemism between 23° S and 26° S, while the southern area showed the highest level of endemism between 27° S and 29° S (Fig. 1).

Latitudinal/altitudinal patterns of species richness

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

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

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

The altitudinal patterns of species richness of the endemic Chilean cacti showed that species richness was negatively related with altitude ($r^2 = 0.362$, $F = 183.33$, $P < 0.001$). Similarly, a second-degree polynomial model showed a significant negative relationship between species richness and altitude, but with a greater portion of the variance explained by the model ($r^2 = 0.427$, $F = 120.95$, $P < 0.001$). Also we detected a significant relationship in the interaction between latitude and altitude in the linear model ($r^2 = 0.370$, $F = 4.42$, $P = 0.036$) and in the polynomial model ($r^2 = 0.362$, $F = 92.52$, $P < 0.001$), indicating that altitudinal patterns of species richness varied along latitudinal bands (Fig. 4).

Latitudinal/altitudinal patterns of distributional ranges of species

The median latitudinal range and latitude were not significantly related in endemic Chilean cacti ($r^2 = -0.014$, $F < 0.001$, $P = 0.987$) (Fig. 5). Moreover, the second-degree polynomial model was not significant ($r^2 = -0.025$, $F = 0.116$, $P = 0.890$). Also we did not detect a significant relationship between the median latitudinal range and altitude in the linear model ($r^2 = 0.03$, $F = 3.213$, $P = 0.08$) or in the polynomial model ($r^2 = 0.017$, $F = 1.632$, $P = 0.203$). A marginal relationship in the interaction between latitude and altitude in the linear model of median latitudinal range was detected ($r^2 = 0.055$, $F = 3.83$, $P = 0.054$), while in the polynomial model the interaction was not significant ($r^2 = 0.015$, $F = 2.066$, $P = 0.155$).

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

Climatic drivers of species richness

The Simultaneous Autoregressive (SAR) model explained 56% of the variance in species richness ($F = 15.785$, $P < 0.001$) (Table 1). Of the 11 explanatory variables, four were significant in the regression analysis (Table 1). The significant explanatory variables were elevation, minimum temperature of the coldest month, mean temperature of wettest quarter and annual precipitation (Table 1). The interaction between annual mean temperature and annual precipitation was not significant.

II.4 DISCUSSION

The biogeographical patterns of the endemic Chilean cacti support the existence of latitudinal and altitudinal gradients of endemism. The shape of the latitudinal gradient is clearly non-linear, supporting the geometric constraints hypothesis, showing a peak of endemism occurring within mid-latitudes (25º-28º S). The altitudinal species richness pattern, however, did support the Rapoport's rule hypothesis, showing a peak of endemism occurring at low altitudes (< 1,000 m.a.s.l.) followed by a monotonic decrease with altitude.

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

The northern species diversification may be closely associated with the Atacama aridity dynamics (Samaniego and Marquet 2009), largely modulated by the Pacific sea-surface temperature anomalies, which in turn have complex multiple effects such as driving the summer rainfall into the Atacama Desert and the adjacent Altiplano (Latorre *et al.* 2002), and closely related to slight changes in the Oceanic fog zone (Cereceda *et al.* 2008). Although in the hyper-arid Atacama Desert (≤ 2 mm of annual precipitations) no cacti species can be found, maximum species richness occurred in two of the 0.5x0.5º cells with very low precipitation (≤ 25 mm). Both cells are located along the coast (25-25.5ºS) in an area with oceanic fog influence that can maintain great biodiversity in spite of the scarce precipitation (Rundel *et al.* 1991; Dillon *et al.* 2009).

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

The southern biogeographic area (27º-36ºS) is associated with semi-arid, xeric and pluvio-seasonal bioclimatic zones of Central Chile. In this area the most important isolation mechanism for many plant groups is thought to have been the glacial refuge dynamics experienced in the complex mountain chains composed by the Andes and Coast Ranges and the transverse mountain chain that crosses Central Chile (Bull-Hereñu *et al.* 2005; Samaniego and Marquet 2009). As annual precipitations and temperature during winter (coldest months) are critical for Cactaceae (Table 1), during glacial maxima cacti may have been confined to relict refugees. Cold has been documented as a barrier for Cactaceae diversity patterns in Argentina and Chile (Kraus 1995; Mourelle and Ezcurra 1997b). Within this southern biogeographical area the genus *Eriosyce* Phil. shows the highest species richness in the Chilean Cactaceae, suggesting that this genus is an apt candidate to test the role of glacial dynamics in speciation.

In this study we showed that geographic hard boundaries imposed in the north by the Atacama Desert, the oldest and most arid region worldwide (~ 150 My), and by the cold and humid conditions in the south (at least ~ 25 My), produced geometric constraints on latitudinal species richness driving the contemporary biogeographical patterns of the endemic Chilean cacti (Hartley *et al.* 2005; Clarke 2006). One of the most remarkable constraints is the hyper-aridity observed in the Atacama Desert, because its consequences are visible in latitudinal and altitudinal patterns of endemic cactus species, which in the most northern part of Chile (i.e. 18- 26° S) has produced a drastic decline in species richness between 1,000-2,750 m.a.s.l. (Fig. 4). Arroyo *et al.* (1988) demonstrated that the aridity of the Atacama Desert diminishes Andean plant species richness between 18°-24° S at altitudes less than 3,750 m.

The geographic constraints imposed by southern temperate conditions also decrease the endemic cacti species richness, where the mixed environmental conditions of high moisture and low temperatures, particularly during the winter, impose severe restrictions on plants with tropical biogeographic origin. Along coastal southern Chile (> 36°S) no cacti can be found, whereas in the Andean Range some non-endemic species survive principally in association with

Patagonian steppes (Kraus 1995). The latitudinal mid-domain effect suggests that the Atacama Desert and the mixed environmental conditions of moisture and cold act as hard barriers in which, in a stochastic perspective, range size and range placement are governed by chance. In a deterministic perspective the Mid-domain effects in species richness patterns arise from biological responses to environmental thresholds rather than a gradual response to environmental gradients (Colwell and Lees 2000).

Altitudinal species richness patterns suggest another type of biological response of the endemic Chilean cacti; species richness shows a sharp altitudinal gradient with richness concentrated in low elevation ranges, supporting Rapoport's rule (Fig. 3). The proposed mechanism explaining this pattern is the existence of a highly variable environment in the higher depauperate zones, in which only species able to tolerate a wide range of climatic conditions can survive at high altitudes (Stevens 1992). The extreme climatic conditions in high altitude zones produce multiple direct detrimental effects on plant species, diminishing their survival. Moreover, indirect synergetic effects such as depressed pollinator richness and visits relative to plant species richness and altitude can impose severe selective pressures affecting the demographic performance of cacti (Arroyo *et al.* 1982; Grytnes and Vetaas 2002).

Distribution ranges of species showed a more complex pattern with wider altitudinal ranges at intermediate altitudes (Fig. 6). Five of the seven species that grow above 1,600 m.a.s.l. occurred in low latitudes, their narrow altitudinal distribution range may be limited by the hyper-arid conditions. On the other hand, the three species with wider altitudinal distribution (> 2.000 meters of amplitude) live at intermediate latitudes without a direct influence of hyper-aridity.

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

Table II.1 Parameter estimates for explanatory variables in the SAR model. * $P < 0.05$; ** $P < 0.001$.

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

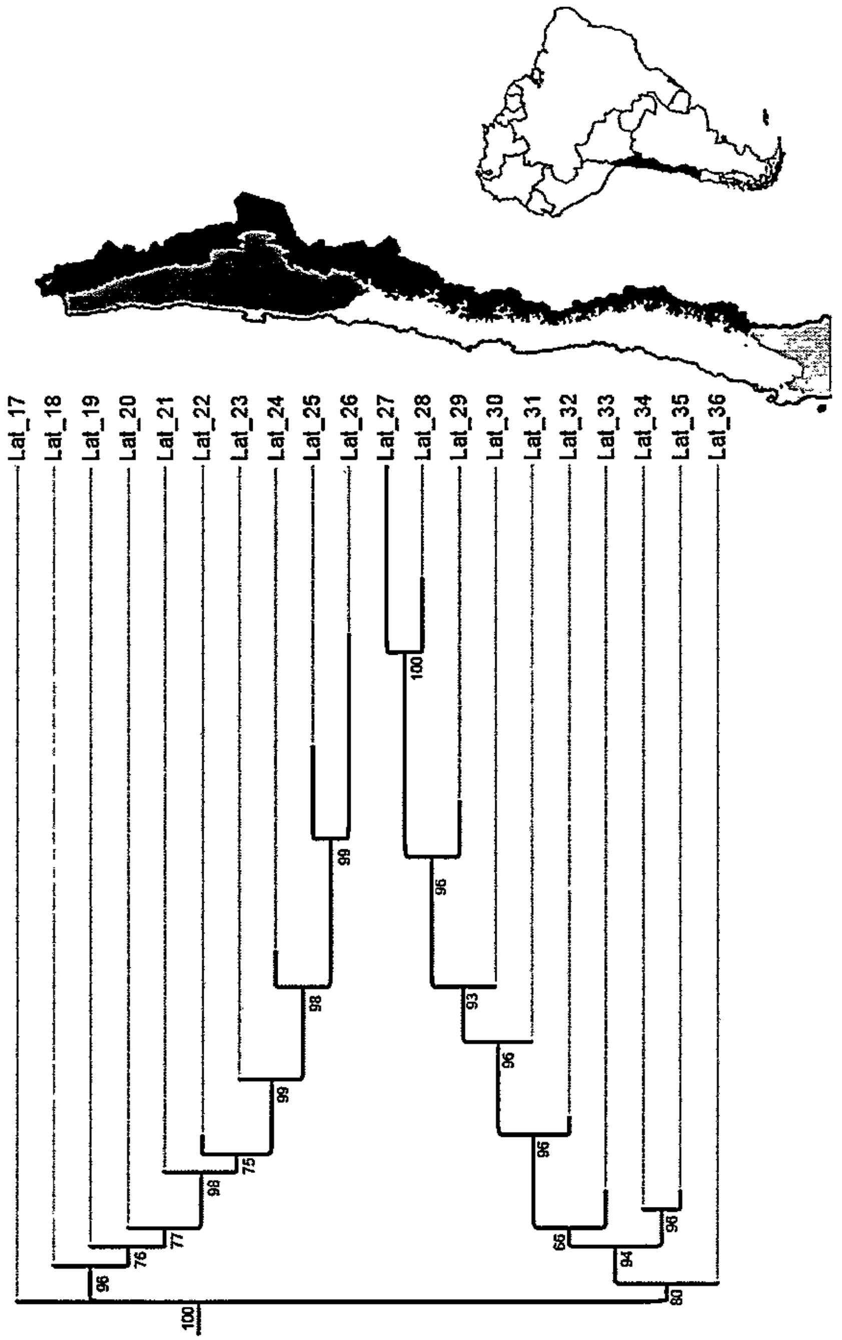

Figure II.1 Bayesian Analysis of Endemism of the distribution of the 72 endemic Chilean cacti in 1° latitude bands. Bayesian posterior probabilities > 50% are indicated above branches. The black area within South America shows the studied area, the black area within Chile shows the Andes Range, the dark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

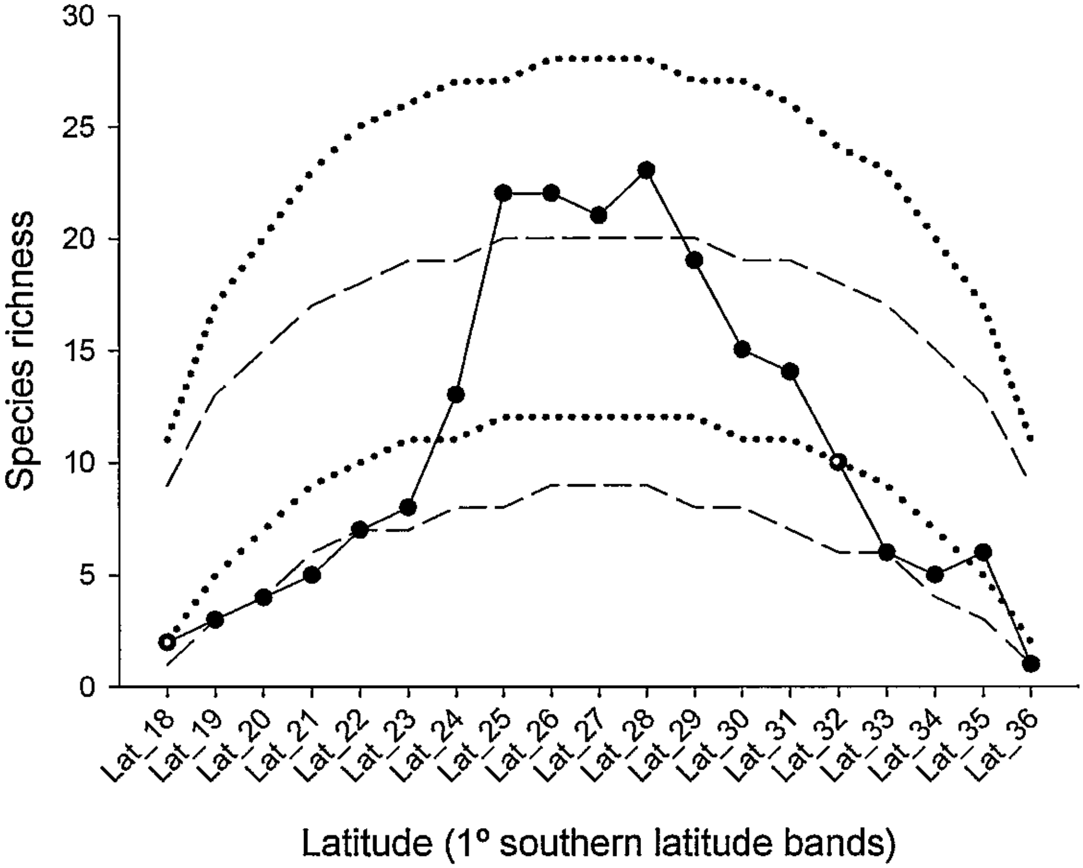

Figure II.2 Species richness found in each band of 1° latitude (black line with data points). The black dashed lines show the 95% prediction curves of sampling without replacement, and the dotted grey lines with replacement.

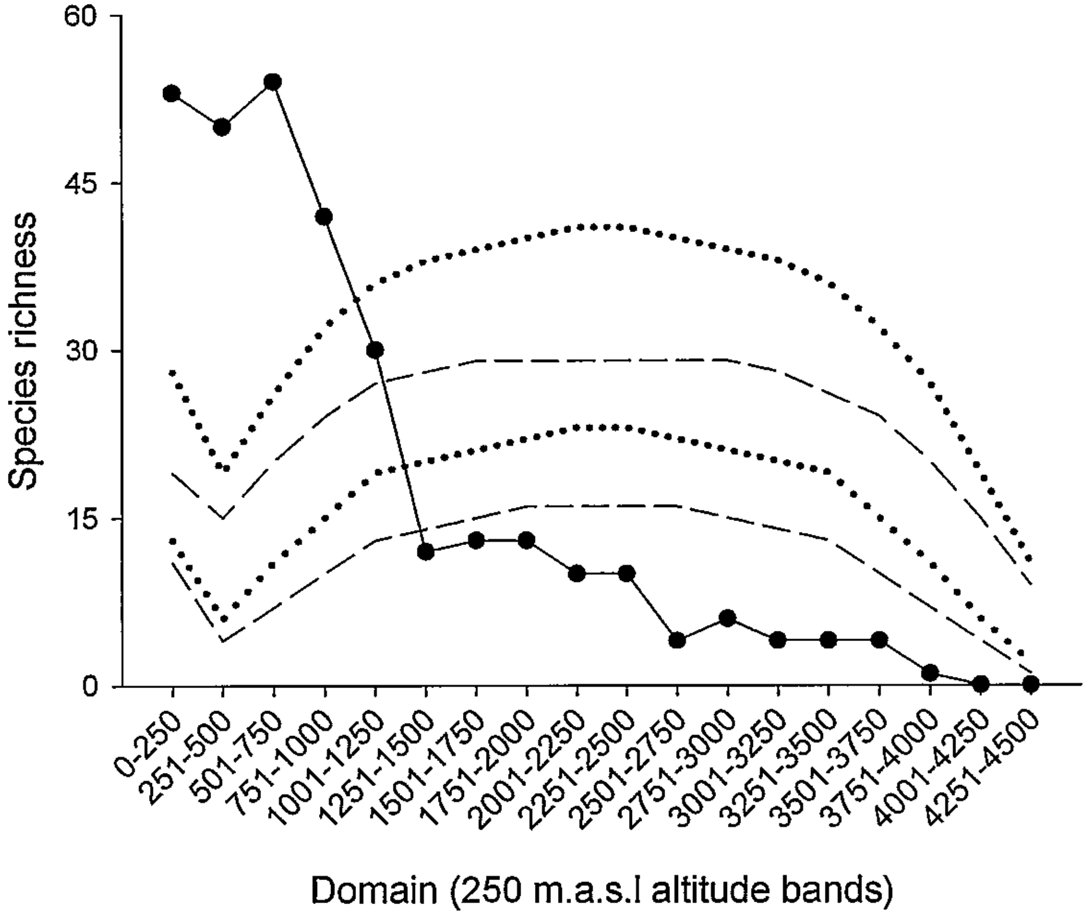

Figure II.3 Species richness found in each 250 m altitude band (black lines with data points). The black dashed lines show the 95% prediction curves of sampling without replacement, and the dotted grey lines with replacement.

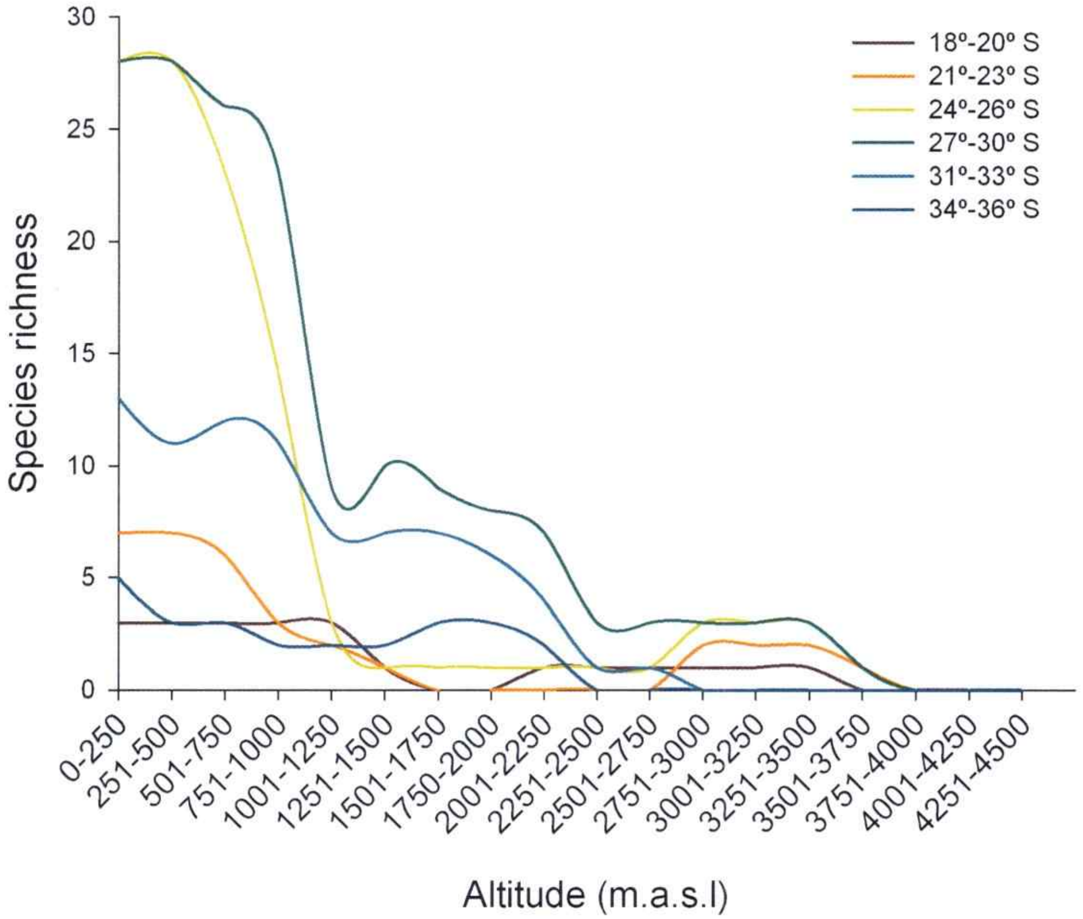

Figure II.4 Altitudinal gradient of species richness of endemic cacti at different latitudinal bands from18º S to 36° S in Chile.

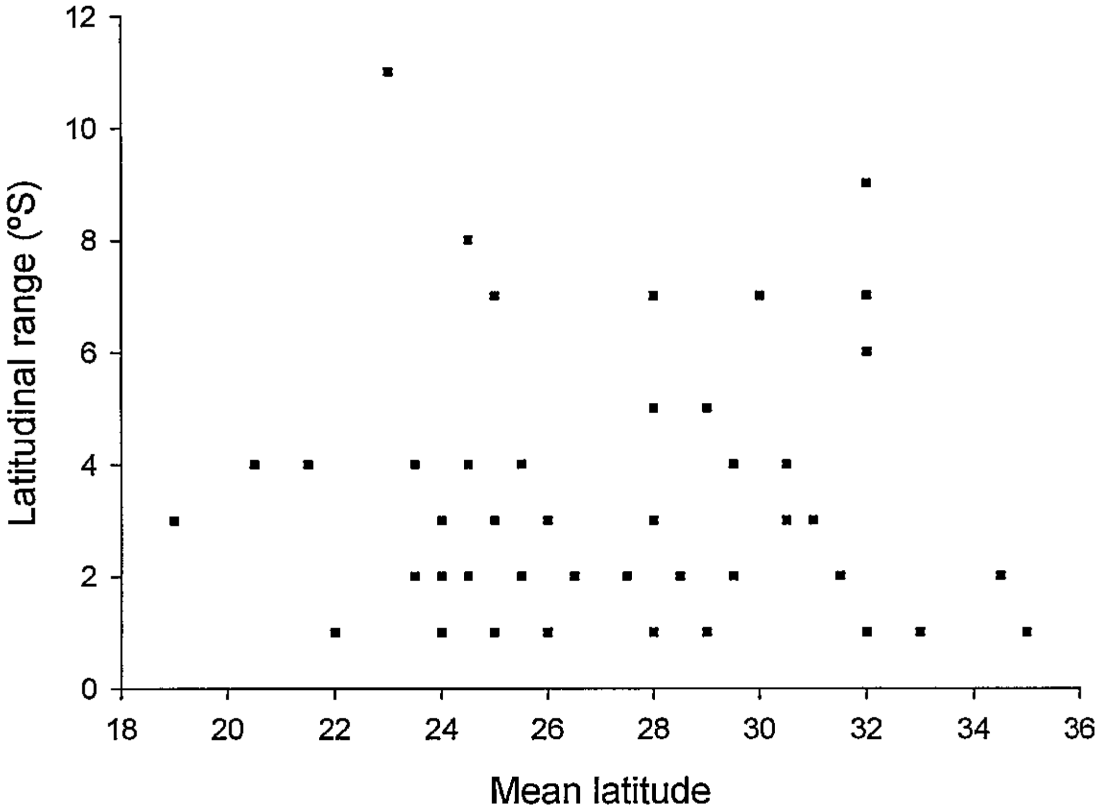

Figure II.5 Relation between median latitudinal range and latitude. Note that are some points overlap, thus making it appear that there are less than 72 points.

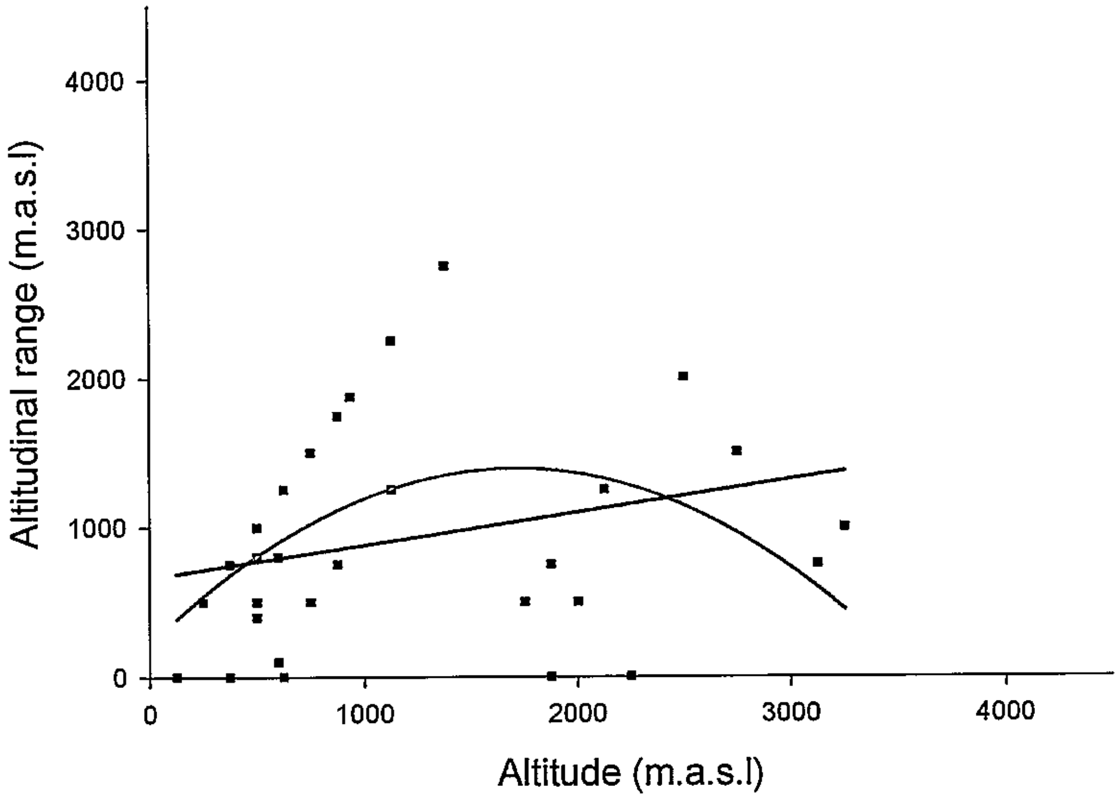

Figure II.6 Relation between median altitudinal range and altitude. The straight line shows the simple regression analysis; the curved line shows the second-degree polynomial model. Note that some points that overlap, thus making it appear that there are less than 72 points.

Appendix II.1 Species and their cohesive range sizes utilized in this study grouped in 1° southern latitude bands.

Species	Latitude 18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
Haageocereus fascicularis	■	■	■																
Eriosyce iquiquensis		■	■	■	■														
Eriosyce recondita			■	■	■	■													
Eriosyce laui					■														
Eulychnia iquiquensis	■	■	■	■	■	■	■	■	■										
Copiapoa solaris						■	■												
Copiapoa ahremephiana							■												
Copiapoa decorticans							■												
Eriosyce paucicostata						■	■	■											
Copiapoa calderana						■	■	■	■										
Copiapoa humilis				■	■	■	■	■	■	■	■								
Maihueniopsis atacamensis				■	■	■	■	■	■	■	■								
Maihueniopsis camachoi				■	■	■	■	■	■	■	■								
Copiapoa angustiflora								■											
Copiapoa aphanes								■											
Copiapoa cinerea							■	■	■										
Copiapoa krainziana								■											
Copiapoa longistaminea								■											
Copiapoa taltalensis								■											
Eriosyce occulta								■											
Eriosyce rodentiophila							■	■	■										
Copiapoa grandiflora								■	■										
Copiapoa laui								■	■										
Copiapoa montana								■	■										
Copiapoa serpentisulcata								■	■										
Eriosyce esmeraldana								■	■										
Eriosyce taltalensis							■	■	■	■									
Copiapoa cinerascens									■										
Copiapoa hypogaea									■										
Copiapoa leonensis									■										
Eriosyce odieri								■	■	■									
Copiapoa marginata									■	■									
Copiapoa megarhiza									■	■									
Eriosyce sociabilis									■	■									
Maihueniopsis colorea									■	■									
Copiapoa dealbata										■	■								
Copiapoa echinoides										■	■								
Copiapoa fiedleriana										■	■								
Copiapoa schulziana											■								
Echinopsis deserticola								■	■	■	■	■	■	■					
Eriosyce confinis										■	■	■							

Appendix II.1 (Continuation).

	Latitude																		
Species	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
Eriosyce crispa											■								
Eriosyce napina										■	■	■							
Eulychnia breviflora									■	■	■	■	■						
Maihueniopsis archiconoidea										■	■	■							
Maihueniopsis crassispina											■								
Maihueniopsis domeykoensis											■								
Miqueliopuntia miquelii										■	■	■							
Eriosyce villosa											■	■							
Eriosyce eriosyzoides										■	■	■	■	■					
Eriosyce simulans												■							
Eulychnia acida										■	■	■	■	■					
Maihueniopsis grandiflora												■							
Maihueniopsis wagenknechtii												■							
Copiapoa coquimbana											■	■	■	■					
Echinopsis coquimbana												■	■						
Eriosyce heinrichiana											■	■	■	■					
Eriosyce aurata										■	■	■	■	■	■	■			
Eriosyce clavata												■	■	■					
Eriosyce senilis												■	■	■	■				
Echinopsis skottsbergii													■	■	■				
Eulychnia castanea													■	■	■				
Eriosyce chilensis														■	■				
Echinopsis chiloensis												■	■	■	■	■	■	■	
Eriosyce garaventae															■				
Eriosyce subgibbosa											■	■	■	■	■	■	■	■	■
Eriosyce curvispina													■	■	■	■	■	■	
Austrocactus spiniflorus																■			
Eriosyce engleri																■			
Echinopsis bolligeriana																	■	■	
Eriosyce aspillagae																	■	■	
Austrocactus philippi																		■	

Appendix II.2 Species and their cohesive range sizes utilized in this study grouped in altitudinal bands of 250-m.

Species	0-250	251-500	501-750	751-1000	1001-1250	1251-1500	1501-1750	1750-2000	2001-2250	2251-2500	2501-2750	2751-3000	3001-3250	3251-3500	3501-3750	3751-4000	4001-4250	4251-4500
Haageocereus fascicularis									■	■	■	■	■	■				
Eriosyce iquiquensis	■	■	■	■														
Eriosyce recondita	■	■	■	■	■													
Eriosyce laui	■	■																
Eulychnia iquiquensis	■	■	■	■	■	■												
Copiapoa solaris	■	■	■	■														
Copiapoa ahremephiana	■	■																
Copiapoa decorticans	■	■	■	■														
Eriosyce paucicostata	■	■	■	■														
Copiapoa calderana	■	■	■	■														
Copiapoa humilis	■	■	■															
Maihueniopsis atacamensis												■	■	■				
Maihueniopsis camachoi												■	■	■	■			
Copiapoa angustiflora		■	■															
Copiapoa aphanes			■	■														
Copiapoa cinerea	■	■	■	■														
Copiapoa krainziana			■	■	■													

Appendix II.2 (Continuation).

Species	0-250	251-500	501-750	751-1000	1001-1250	1251-1500	1501-1750	1750-2000	2001-2250	2251-2500	2501-2750	2751-3000	3001-3250	3251-3500	3501-3750	3751 - 4000	4001 - 4250	4251 - 4500
Copiapoa taltalensis	■	■																
Eriosyce occulta	■	■	■															
Eriosyce rodentiophila	■	■	■	■														
Copiapoa grandiflora	■	■	■	■														
Copiapoa laui	■	■	■	■														
Copiapoa montana	■	■	■	■	■													
Copiapoa serpentisulcata	■	■	■															
Eriosyce esmeraldana	■	■																
Eriosyce taltalensis	■	■	■	■														
Copiapoa cinerascens	■	■																
Copiapoa hypogaea	■	■	■															
Copiapoa leonensis		■	■	■														
Eriosyce odieri	■	■	■	■														
Copiapoa marginata	■	■																
Copiapoa megarhiza	■	■	■															
Eriosyce sociabilis	■	■																
Maihueniopsis colorea							■	■	■	■	■	■	■	■				
Copiapoa dealbata	■	■																
Copiapoa echinoides	■	■	■															

Appendix II.2 (Continuation).

Species	0-250	251-500	501-750	751-1000	1001-1250	1251-1500	1501-1750	1750-2000	2001-2250	2251-2500	2501-2750	2751-3000	3001-3250	3251-3500	3501-3750	3751-4000	4001-4250	4251-4500
Copiapoa fiedleriana	■																	
Copiapoa schulziana			■															
Echinopsis deserticola	■	■	■	■														
Eriosyce confinis	■	■	■	■														
Eriosyce crispa		■																
Eriosyce napina	■	■	■	■														
Eulychnia breviflora	■	■	■															
Maihueniopsis archiconoidea							■	■	■	■	■							
Maihueniopsis crassispina		■	■															
Maihueniopsis domeykoensis			■															
Miqueliopuntia miquelii	■	■	■	■														
Eriosyce villosa	■	■	■	■														
Eriosyce eriosyzoides	■	■	■	■	■	■	■	■										
Eriosyce simulans	■	■																
Eulychnia acida	■	■	■	■	■	■												
Maihueniopsis grandiflora								■	■									
Maihueniopsis wagenknechtii							■	■	■									
Copiapoa coquimbana	■	■	■	■	■	■	■	■										
Echinopsis coquimbana	■	■	■	■	■	■												

Appendix II.2 (Continuation).

Species	0-250	251-500	501-750	751-1000	1001-1250	1251-1500	1501-1750	1750-2000	2001-2250	2251-2500	2501-2750	2751-3000	3001-3250	3251-3500	3501-3750	3751-4000	4001-4250	4251-4500
Eriosyce heinrichiana	■	■	■	■														
Eriosyce aurata	■	■	■	■	■	■	■	■	■	■	■							
Eriosyce clavata	■	■	■	■														
Eriosyce senilis			■	■	■	■	■											
Echinopsis skottsbergii	■	■	■	■														
Eulychnia castanea	■																	
Eriosyce chilensis	■																	
Echinopsis chiloensis	■	■	■	■	■	■	■	■	■									
Eriosyce garaventae									■									
Eriosyce subgibbosa	■	■	■															
Eriosyce curvispina	■	■	■	■	■	■	■	■	■									
Austrocactus spiniflorus							■	■										
Eriosyce engleri								■										
Echinopsis bolligeriana	■																	
Eriosyce aspillagae	■																	
Austrocactus philippi								■	■									

Appendix II.3 Literature used to defined species distributions.

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Appendix II.4 Number of records per species.

Species	Number of records
Austrocactus philippi	1
Austrocactus spiniflorus	2
Copiapoa ahremephiana	5
Copiapoa angustiflora	1
Copiapoa aphanes	1
Copiapoa calderana	15
Copiapoa cinerascens	19
Copiapoa cinerea	88
Copiapoa coquimbana	41
Copiapoa dealbata	10
Copiapoa decorticans	4
Copiapoa echinoides	15
Copiapoa fiedleriana	14
Copiapoa grandiflora	19
Copiapoa humilis	22
Copiapoa hypogaea	6
Copiapoa krainziana	5
Copiapoa laui	8
Copiapoa leonensis	6
Copiapoa longistaminea	11
Copiapoa marginata	16
Copiapoa megarhiza	6
Copiapoa montana	6
Copiapoa schulziana	1
Copiapoa serpentisulcata	19
Copiapoa solaris	22
Copiapoa taltalensis	19
Echinopsis bolligeriana	3
Echinopsis chiloensis	208
Echinopsis coquimbana	49
Echinopsis deserticola	14
Echinopsis skottsbergii	27
Eriosyce aspillagae	9
Eriosyce aurata	145
Eriosyce chilensis	12
Eriosyce clavata	12
Eriosyce confinis	46
Eriosyce crispa	3
Eriosyce curvispina	136
Eriosyce engleri	1
Eriosyce eriosyzoides	20
Eriosyce esmeraldana	8
Eriosyce garaventae	3
Eriosyce heinrichiana	56

Appendix II.4 (Continuation).

Species	Number of records
Eriosyce iquiquensis	5
Eriosyce laui	1
Eriosyce napina	34
Eriosyce occulta	3
Eriosyce odieri	26
Eriosyce paucicostata	10
Eriosyce recondita	9
Eriosyce rodentiophila	11
Eriosyce senilis	23
Eriosyce simulans	1
Eriosyce sociabilis	3
Eriosyce subgibbosa	113
Eriosyce taltalensis	45
Eriosyce villosa	10
Eulychnia acida	210
Eulychnia breviflora	32
Eulychnia castanea	24
Eulychnia iquiquensis	27
Haageocereus fascicularis	13
Maihueniopsis archiconoidea	1
Maihueniopsis atacamensis	15
Maihueniopsis camachoi	21
Maihueniopsis colorea	9
Maihueniopsis crassispina	2
Maihueniopsis domeykoensis	2
Maihueniopsis grandiflora	2
Maihueniopsis wagenknechtii	1
Miqueliopuntia miquelii	9

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CHAPTER III: PHYLOGENETICS AND PREDICTIVE DISTRIBUTION MODELING PROVIDE INSIGHTS INTO THE GEOGRAPHIC DIVERGENCE OF *ERIOSYCE* SUBGEN. *NEOPORTERIA* (CACTACEAE).

III.1 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 using phylogenetic 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 to climatic tolerances.

KEY WORDS: Chile, morphology, diversification, ecological niche modeling, vicariance, speciation.

II.2 INTRODUCTION

Understanding the processes that lead to the origin of new taxa is a fundamental goal of evolutionary biology (Darwin 1859, Futuyma 2009). In this sense, the essential role of geographic isolation driving a 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 (such as 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 Glor 2003), while growing in sympatry ecological mechanisms, such as 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 allow an understanding of the mechanism(s) underlying the evolutionary and the ecological process that splits an ancestral species into new lineages (Wiens 2004b). These views may be addressed by 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), as 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 present 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 various 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 funnel-form to tubular fuchsia-coloured flowers are hummingbird-pollinated and their stems get 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 particular, the gross morphological affinities of *E. chilensis* and *E. taltalensis* subsp. *taltalensis* with *Neoporteria* and *Horridocactus* have challenged their infrageneric postitions (Britton and Rose 1992, Kattermann 1994, Walter 2008) (Fig. 1, appendix 1).

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* subsp. *taltalensis* within *Eriosyce sensu lato* by using molecular and morphological data. As none of the previous taxonomic or phylogenetic proposals have been spatially evaluated, and 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 means of comparing the predicted distribution overlap between sister taxa using predictive distribution modeling.

III.3 MATERIALS AND METHODS

Plant material

The morphological dataset was obtained 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 of *C. brevistylus* was taken from cultivated ex-habitat specimens. Most of the characters of the epidermis, hypodermis, cortex and pith were adopted from Nyffeler and Eggli (1997). Morphological characters associated with flowers were emphatized because

Neoporteria is characterized by a wide interespecific variation in flower shape compare to *Eriosyce sensu lato* (Fig. 1) (Walter 2008).

Taxon sampling

The sampling of the *Eriosyce* taxa used in this study was based on the classification in Kattermann (1994, 2001) as it is widely used and allowed us comparisons with the first phylogenetic hypothesis put forward for *Eriosyce sensu lato* Twelve distinct operational taxonomic units from subsection *Neoporteria* at species and infraspecific levels were chosen as an ingroup in all the phylogenetic analyses (recent taxonomical proposals of ingroups and outgroups are available in the electronic supplementary material, appendix 1). Infraspecific taxa were included for two reasons: firstly, because of the problem of polymorphic character states within species (Nixon and Davis 1991). Secondly, 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; see 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 *trnL-trnF* and nine in the *rpl32-trnL* data set. In addition to that, we included distantly related *Corryocactus brevistylus* (tribe *Phyllocacteae* subtribe *Corryocactinae*) in all analyses, and *Neowendermannia chilensis* in analyses that included *rpl32-trnL*. 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 showed the same characteristics 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 characters 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 10000 rpm for 5 min to remove mucilage (Setoguchi *et al.* 1998). Total genomic DNA was isolated using the CTAB procedure described by Doyle and Doyle (1987). Two genes were amplified using standard primers and protocol (*rpl32-trnL*$^{(UAG)}$: Shaw *et al.* 2007; *trnL-trnF:* Nyffeler 2002). When multibands were presented in the gel, the bands corresponding to the expected by literature size of the gene 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 of 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$0) using an automated thermal cycler and standard PCR protocols, with PCR cycling time as follows: *rpl32-trnL*: 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; *trnL-trnF:* denaturation at 94°C for 4 min, followed by 40 cycles of 94°C for 30 sec, 46°-54°C for 1 min, and 72°C for 90 sec, 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.

Phylogenetic analyses were conducted for each individual partition (morphology, *rpl32-trnL* and *trnL-trnF*) and for some partition combinations (*rpl32-trnL + trnL-trnF, rpl32-trnL +trnL-trnF*+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, 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 (*rpl32-trnL + trnL-trnF*) and the partition that included both genes and morphology (*rpl32-trnL +trnL-trnF*+morphology). For each separate and combined analysis, we ran two replicate searches for 5 x 10^6 generations each, sampling every 1000 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 allows for the 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.

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. 2). 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 analysing 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*.

III.4 RESULTS

Phylogenetic relationships

The morphological data placed *E. islayensis* and *E. aurata* in a basal polytomy together with *Corryocatus brevistylus* (Fig. 3). All the *Neoporteria sensu stricto* taxa were included in a single well-supported clade that also comprised *E. taltalensis* subsp. *taltalensis* 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* subsp. *taltalensis/E. sociabilis, E. senilis* subsp. *senilis*/subsp. *coimasensis* and *E. subgibbosa* subsp. *clavata*/subsp. *nigrihorrida*, while 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. 3), the basal species remained in the same position; in the *rpl32-trnL* partition that included *Neowerdermannia chilensis,* the latter was placed between *E. aurata* and *E. curvispina* subsp. *curvispina*. The most important difference between the *trnL-trnF* and *rpl32-trnL* analyses was the placement of *E. sociabilis* and *E. taltalensis* subsp. *taltalensis*: in the former analysis *E. taltalensis* subsp. *taltalensis* and *E. sociabilis* were placed within the *Neoporteria* clade, while the latter placed it in the sister clade to *Neoporteria sensu stricto* compromising *E. odieri, E. krausii, E. paucicostata* and the rest of the taxa of the *E. taltalensis* complex. This difference might be explained by the fact that the *rpl32-trnL* partition included more taxa compared to the *trnL-trnF* 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* subsp. *taltalensis* were excluded from the *Neoporteria* clade (Fig. 4). 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 *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. 5). 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. 5a). 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. 5b). The group comprising *E. subgibbosa* subsp. *vallenarensis*, subsp. *wagenknechtii* and *E. villosa* showed a similar allopatric pattern (occurrence probabilities < 0.5) (Fig. 5c). *E. subgibbosa* var. *subgibbosa* and var. *castanea* were shown to be separated by a distance of some 20 km (Fig. 5d).

In addition to that, predictive distribution modeling indicated that *E. subgibbosa* var. *litoralis* and *E. curvipina* var. *mutabilis* has null overlap between them, while the probability of an overlap of the latter species' distribution with *E. subgibbosa* var. *subgibbosa* was high (Fig. 6a). The overlap between these species matched with 77.2% of the distribution extent of *E. chilensis* ($P >0.75$; Fig. 6b).

III.5 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, though at different taxonomic ranks (genus, subsection, subgroup, subgenus; see 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* (see Walter 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 represent 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 wihin *Horridocactus /Pyrrhocactus* or *Neoporteria* (see 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, while in the morphology-based tree it was placed basal to all ingroup taxa, most probably due to the various "pollination syndrome characters" in our morphological data set (Fig. 1). This assumption coincides with Styles (1981) reporting that nearly all hummingbird flowers of North America have evolved from insect-pollinated species). On the other hand, in Nyffeler and Eggli's analysis (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 subsection *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), as *E. subgibbosa* subsp. *subgibbosa* was never grouped in one clade. Our analysis based on the combined molecular markers (Fig. 4a) suggests the existence of at least three distinct entities within Kattermann's (1994) broad concept of *E. subgibbosa*: (i) *E. subgibbosa* var. *subgibbosa* / var *castanea*, (ii) *E. subgibbosa* subsp. *nigrihorrida* / subsp. *clavata,* and (iii) *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 proposed by Walter (2008). A future study would probably have to sample inter- and infra-populational variability to resolve relationships in this subclade.

The analyses based on the combined molecular (Fig. 4a) and the molecular/morphological data (Fig. 4b) excluded *E. sociabilis* and *E. taltalensis* subsp. *taltalensis* from the *Neoporteria* clade, while our morphological and *trnL-trnF* (Fig. 3a-b) data included it in this clade. The cause of this inconsistency might be the less dense taxon sampling in the *trnL-trnF* partition compared with the *rpl32-trnL* 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 like the fuchsia-red colour, the size or the narrow funnel-form hypanthia, but the inner perianth segments of *E. sociabilis* are 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 polyphyletic.

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

Predictive distribution modeling and the geography of divergence

Analyses of the degree of geographic overlap between sister taxa obtained from the phylogenetic analysis showed that most of the sister taxa are spatially segregated entities or show minimal overlap, suggesting that allopatric divergence is a widespread phenomenon in *Neoporteria* (Fig. 5). 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*), showed any degree of predictable geographic overlap (Fig. 5).

Although it was not part of the aim 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 to peripatric speciation (Losos and Glor 2003), however, our sister taxa have similar range sizes (Figs 5). This suggests that their divergence was originated by an allopatric vicariant event (probably due to 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 historic climate changes affecting different of taxonomic groups of plants (Wara *et al.* 2005, Latorre *et al.* 2002, Houston 2006, Luebert and Pliscoff 2006). Other vicariant diversification associated to climate changes are *Heliotropium* section Cochranea (Miers) Kuntze (Heliotropiaceae), *Nolana* L. ex L.f. (Solanaceae), *Moscharia* Ruiz et Pav. (Asteraceae) and *Tillandsia* L. (Bromeliaceae). Although their diversification process were initated at different geological eras, changes in aridity had always contributed to their allopatric divergence (Katinas and Crisci 2000, Luebert and Wen 2008, Dillon *et al.* 2009, Zizka *et al.* 2009, Luebert *et al.* 2011).

The predicted spatial separation between *E. senilis* subsp. *senilis* / *E. senilis* subsp. *coimasensis* is about 50-100 km, suggesting that both taxa may belong to different evolutionary lineages and even may 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 the latitudes of 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, based on 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 only 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 a genetic proximity and a complex scenario of species reproductive interactions. Hibrization is a porwrfull evolutionary force in plants and cactus are not an exception (Stebbins 1959, Rowley 1994, Seehausen 2004), further study is needed to test *E. chilensis'* reticular origin, as well as extensive genetic sampling at population level and detailed evaluations of the reproductive biology of the four species.

The 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 were mostly originated by historical vicariant events that resulted in the splitting of one common ancestor into two new taxa. The role of pollinators in driving speciation appears to be less important than geographic isolation caused by climatic tolerances, although, less frequently, pollinator guilds and the phenology of species might play a role in reticular speciation.

Table III.1 List of taxa, their infragenenéric categories used in Kattermann (1994), their acronyms used in the phylogenetic and distribution modelling analyses, their latitudinal distribution in Chile and the plant material used in this study. 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). Herbarium collection specimens examined are given in brackets, and when Genbank codes apply they are given in square brackets [trnL-trnF, rpl32-trnL], as well. CONC= Universidad de Concepción and SGO= Museo Nacional de Historia Natural.

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.
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, Pichidanguí. 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.
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	28º-29º 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.

Table III.2 Characters and character states for the phylogenetic 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 colour	[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	[0] yes	[1] no			

	simultaneous				
17	Style colour	[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	Colour of innermost perianth segments	[0] white or yellow	[1] bicolorous: inferior part whitish, superior fuchsia	[2] fuchsia	[3] red
27	Flower colour	[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 um	[1] 31-40 um	[2] 41-70 um	
30	Secondary cell divions of epidermis cells	[0] Only periclinal	[1] periclinal or oblique	[2] not applicable	

31	Number of periclinal and oblique secondary cell divisons in non-papillate cells	[0] none	[1] few	[2] many	[3] not applicable
32	Number of periclinal and oblique secondary cell divisons 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 um	[1] 60-110 um	[2] 140-350 um	[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	Colour 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).

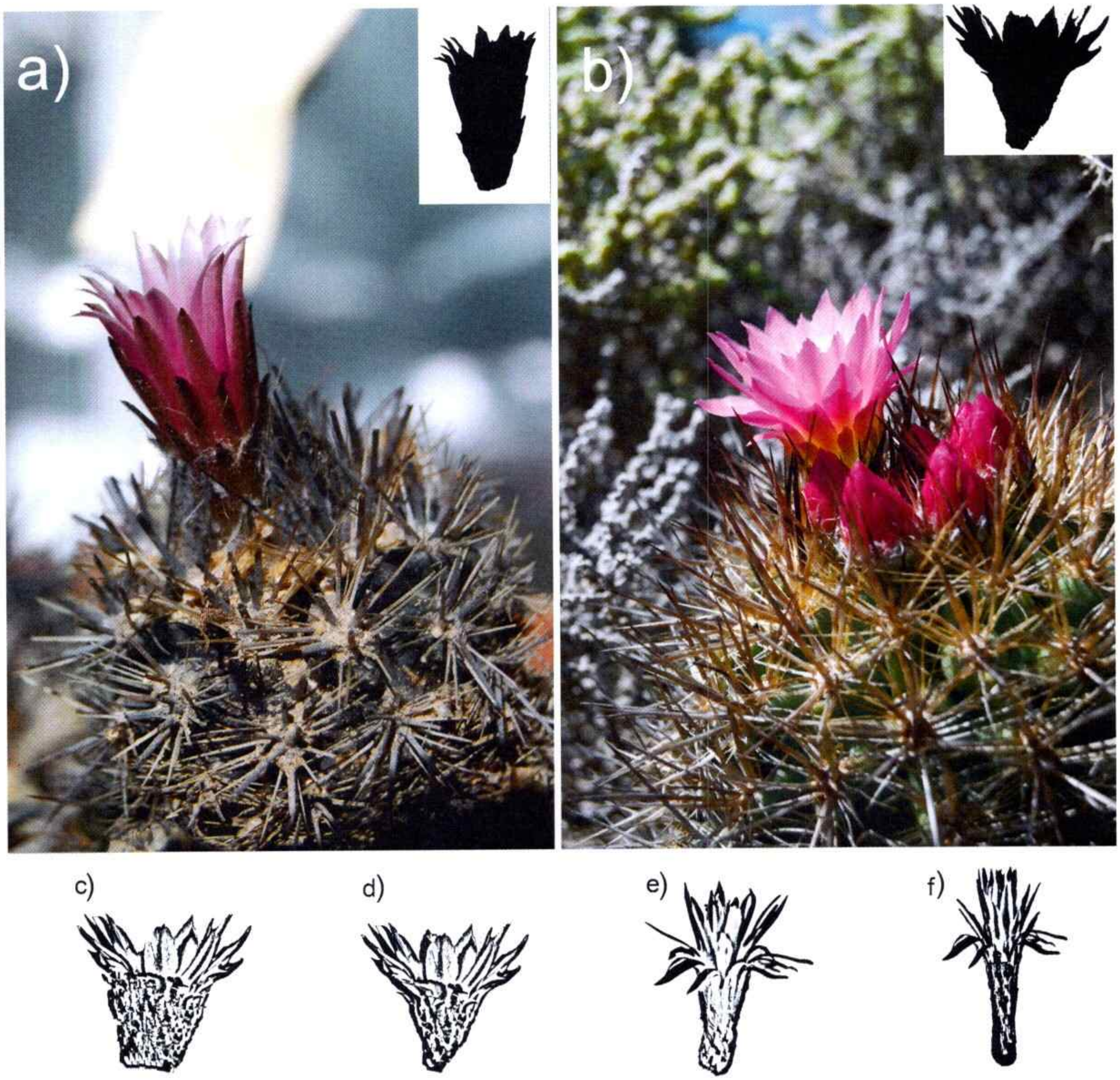

Figure III.1 Examples of morphological variation in the flowers within *Eriosyce sensu lato.* Photographs show the red- fuchsia colors of the flowers of *Eriosyce taltalensis* var. *taltalensis* (a) and *E. chilensis* (b). The white square at top-right show the shape of the flower: narrow funnel form (a) and funnel form (b). Illustrations at the bottom show the evolutionary change in the shape and tepals attitude among *E. aurata* (c), *E. chilensis* (d), *E. subgibbosa* subsp. *nigrihorrida* and *E. senilis* subsp. *senilis* (f).

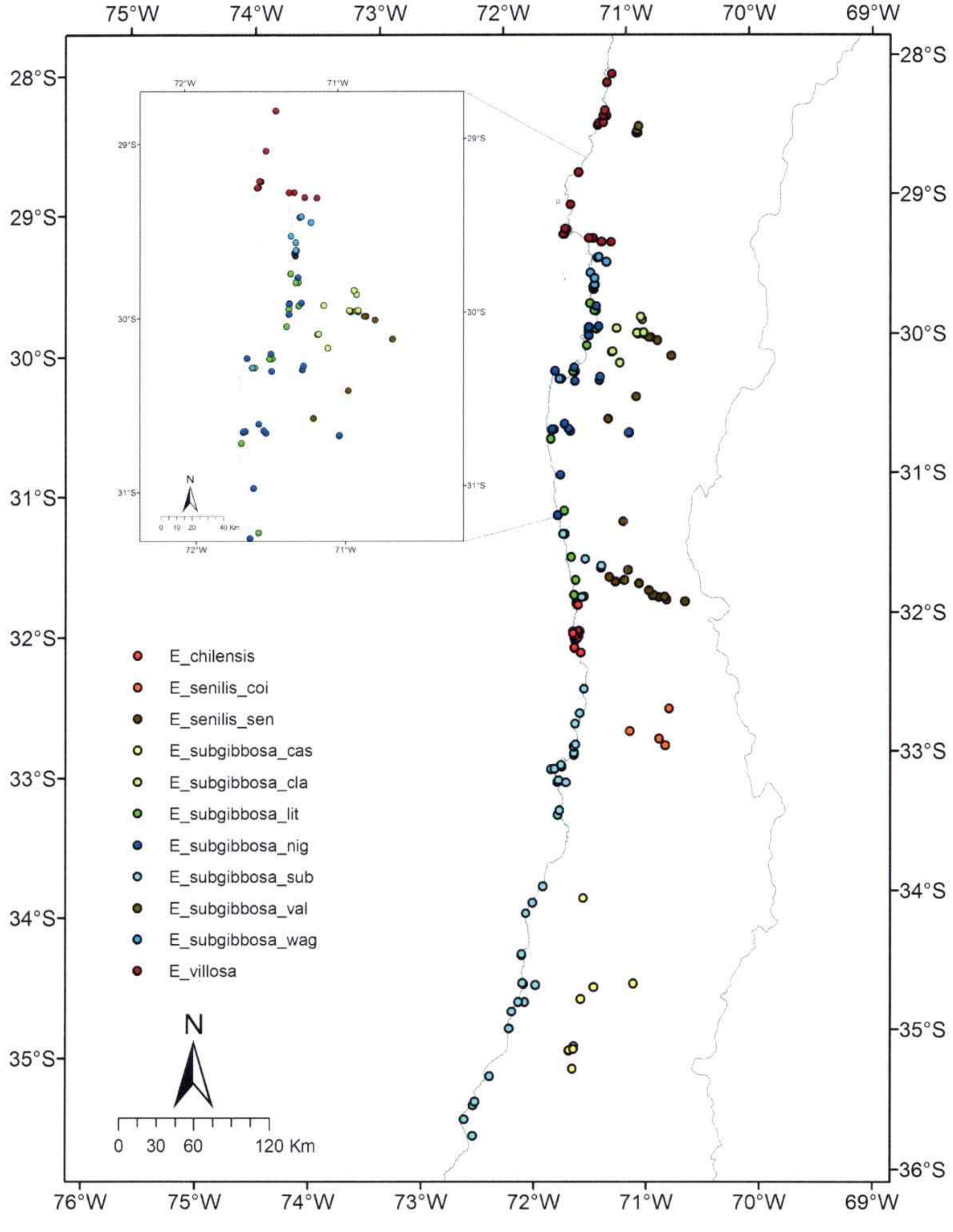

Figure III.2 Population localities of *Eriosyce* subgen. *Neoporteria* compiled from field excursions, literature and Chilean herbaria.

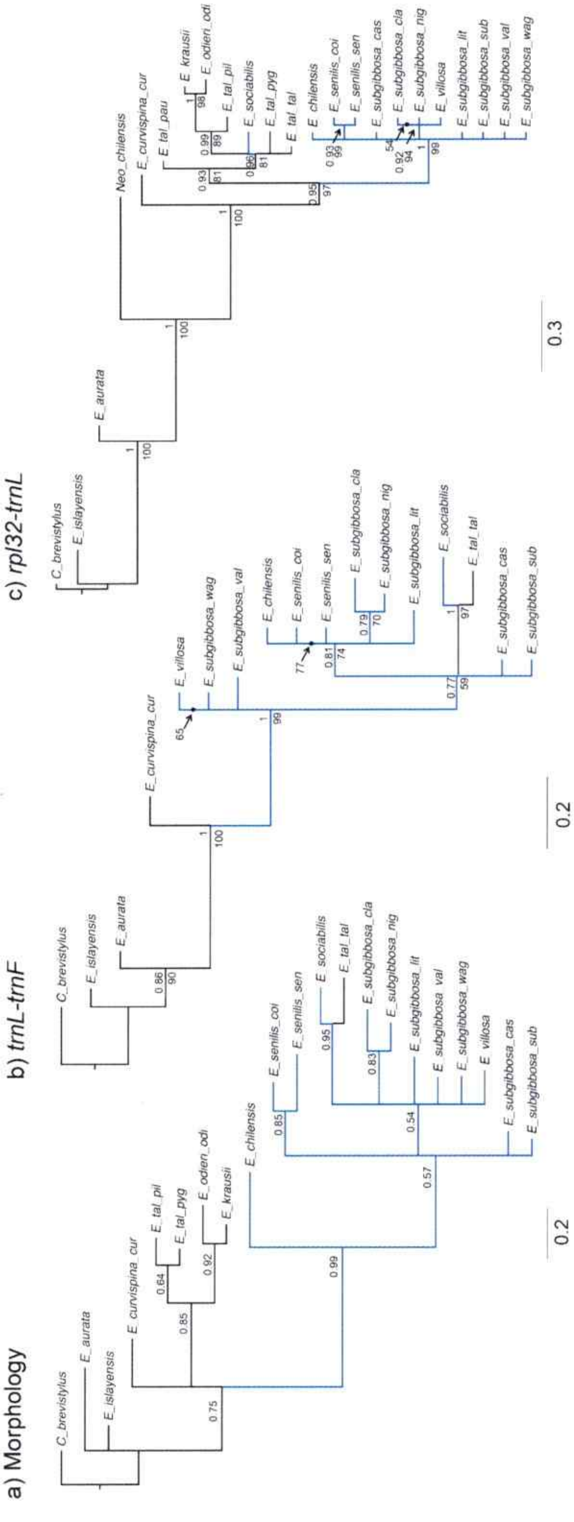

Figure III.3 Phylogeny of *Eriosyce* subgen. *Neoporteria* based on separate Bayesian analysis of morphology, and separate Bayesian and maximum likelihood analyses of molecular data based on trnL-trnF and rpl32-trnL (chloroplast DNA).

Numbers above branches indicate a posteriori Bayesian support; those below indicate ML bootstrap support. Filled black circles indicate nodes that were supported with >50% of bootstrap support in ML analyses.

a) *rpl32-trnL + trnL-trnF*

b) *rpl32-trnL+trnL-trnF*+morphology

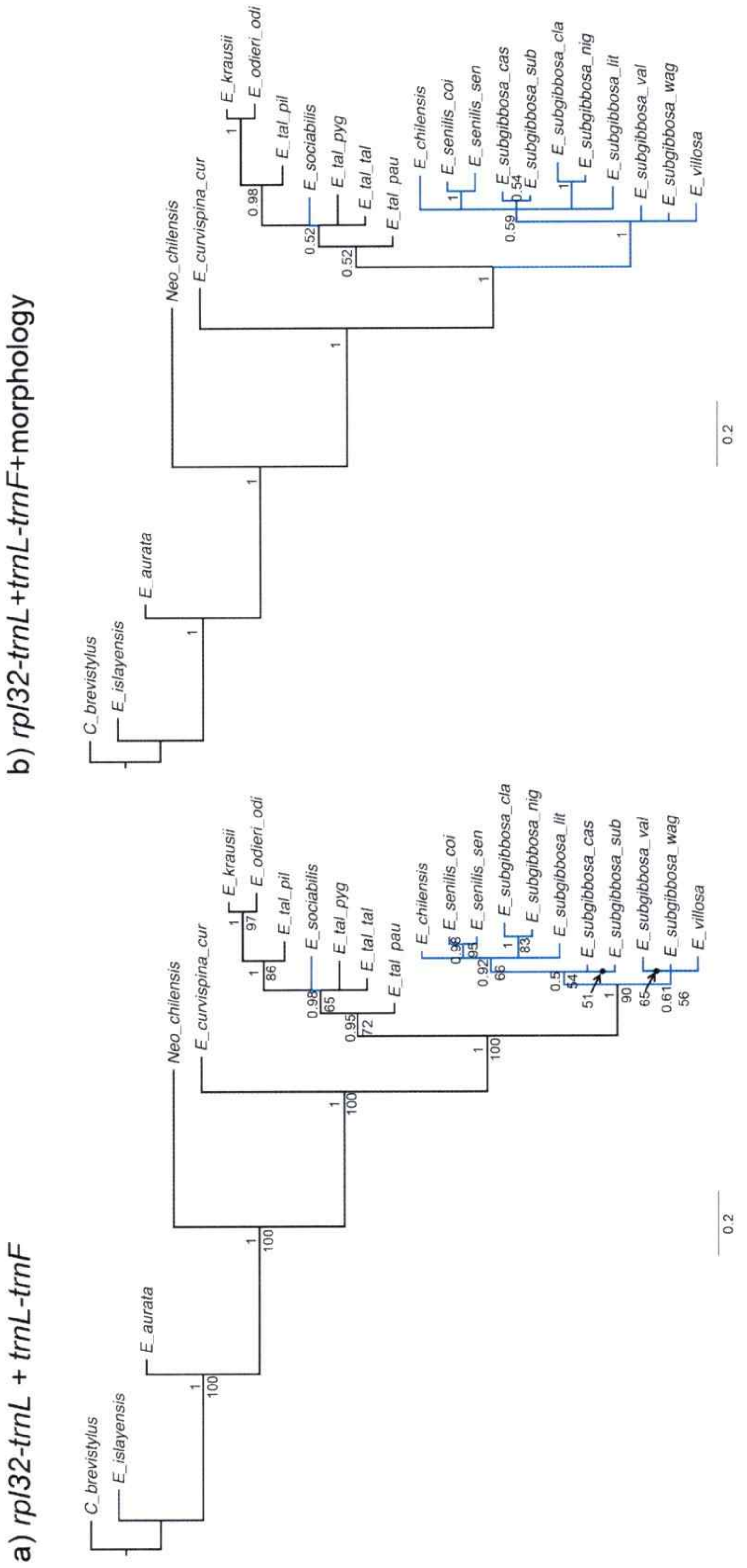

Figure III.4 Phylogeny of *Eriosyce* subgen. *Neoporteria* based on combined

Bayesian and maximum likelihood analyses of molecular data: trnL-trnF + rpl32-trnL (chloroplast DNA), and combined Bayesian analysis of molecular and morphological data. Numbers above branches indicate a posteriori Bayesian support; those below indicate ML bootstrap support. Filled black circles indicate nodes that were supported with >50% of bootstrap support in ML analyses.

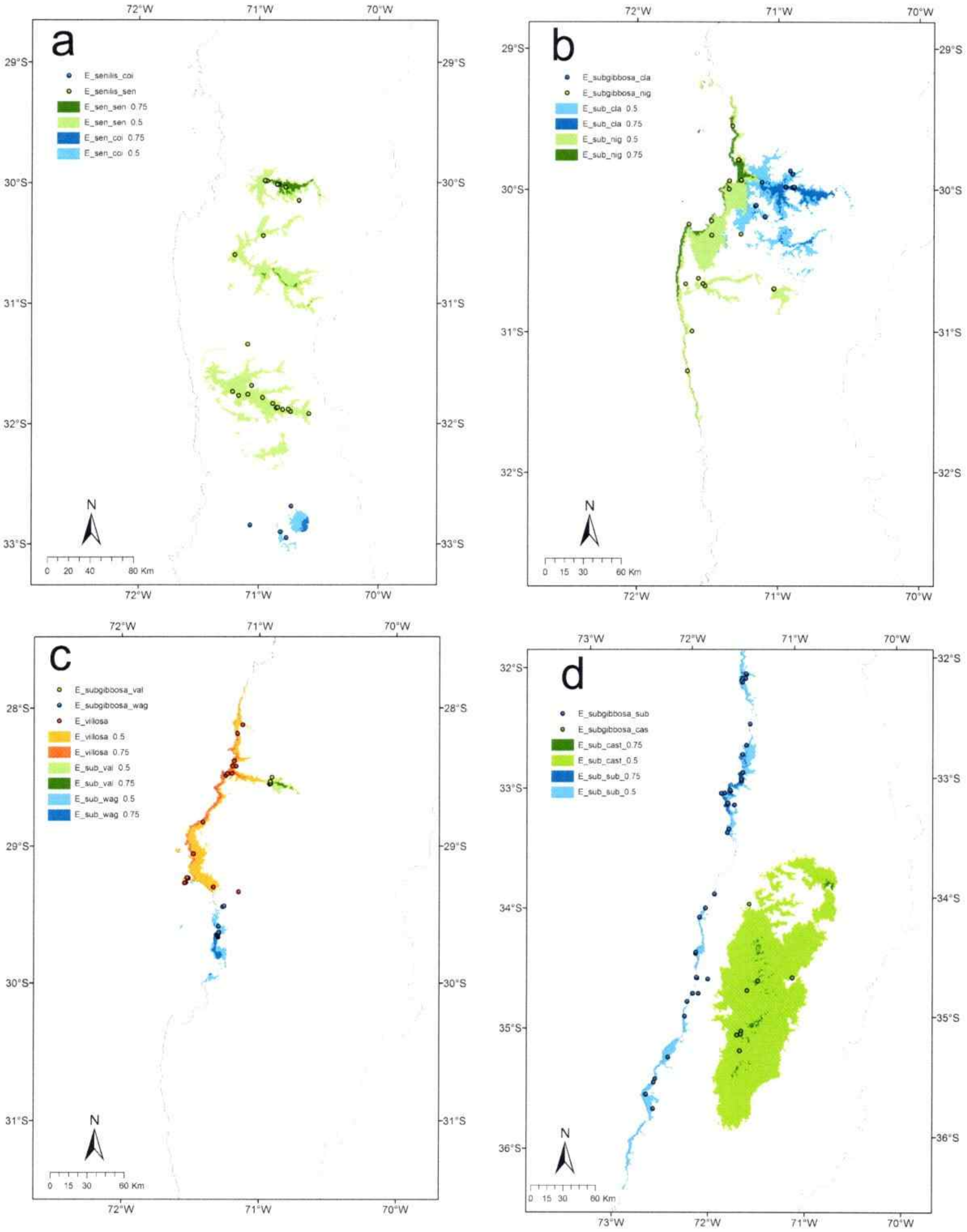

Figure III.5 Predicted geographic distributions of selected sister taxa of *Eriosyce* subgen. *Neoporteria* based on ecological niche modeling. Circles are documented localities for each taxon. a) *E. senilis* subsp. *senilis* and subsp. *coimasensis*. b) *E.*

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.*

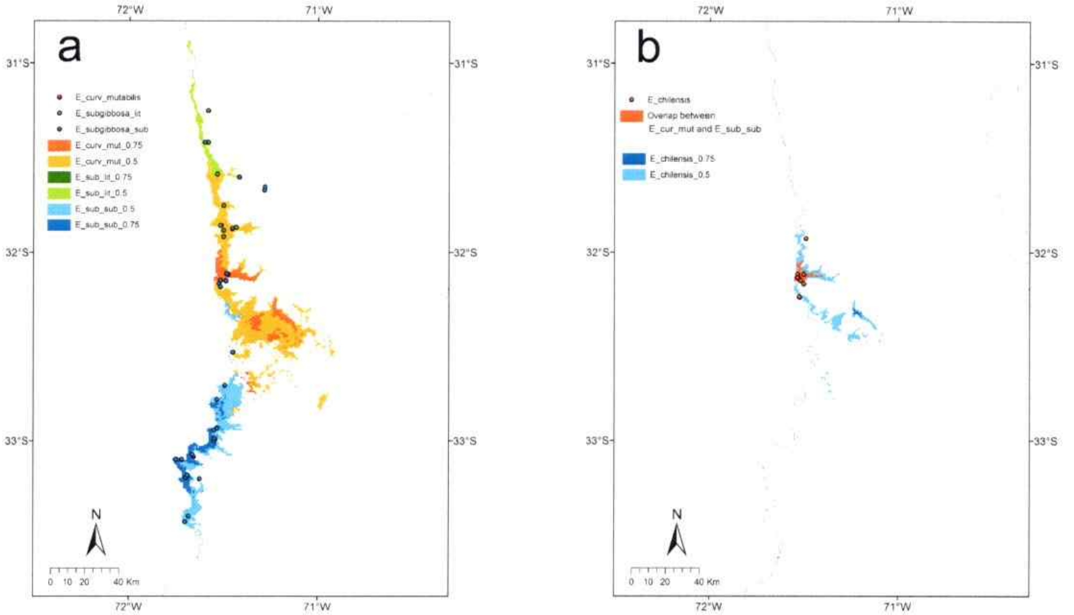

Figure III.6 Predicted geographic distributions of two subsections within *Eriosyce* whose distributions overlap in central coastal Chile. Circles are documented localities for each taxon. We evaluated the probability of co-ocurrence of one *Horridocactus* and two *Neoporteria* taxa to determine if the estimated overlaps matched with *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*.

Appendix III.1 Synopsis of recently proposed classifications of the 21 *Eriosyce s. l.* taxa sampled for this study.

Hoffmann (1989)	Kattermann (1994, 2001)	Hoffmann & Walter (2005)	Hunt *et al.* (2006)	Walter (2006, 2008)	Zuloaga *et al.* (2008)
Neoporteria sensu stricto	***Eriosyce subsect. Neoporteria***	***Eriosyce subgen. Neoporteria***	***Eriosyce subgroup Neoporteria***	***Eriosyce subgen. Neoporteria***	***Neoporteria***
	E. chilensis		*E. chilensis*	(Infrageneric placement undecided)	
N. nidus	*E. senilis* subsp. *senilis*	*E. senilis* subsp. *senilis*	*E. senilis* subsp. *senilis*	*E. senilis* subsp. *senilis*	*N. nidus*
N. nidus var. *coimasensis*	*E. senilis* subsp. *coimasensis*	*E. senilis* subsp. *coimasensis*	*E. senilis* subsp. *coimasensis*	*E. senilis* subsp. *coimasensis*	*N. nidus*
N. sociabilis	*E. sociabilis*	*E. sociabilis*	*E. sociabilis*	*E. sociabilis*	*N. sociabilis*
N. subgibbosa var. *subgibbosa*	*E. subgibbosa* subsp. *subgibbosa*	*E. subgibbosa* subsp. *subgibbosa*	*E. subgibbosa* subsp. *subgibbosa*	*E. subgibbosa*	*N. subgibbosa*
N. subgibbosa var. *litoralis*	*E. subgibbosa* subsp. *subgibbosa* var. *litoralis*	*E. subgibbosa* subsp. *subgibbosa* var. *litoralis*	*E. subgibbosa*	close to *E. villosa* (taxonomic rank undecided)	*N. subgibbosa*
N. castanea	*E. subgibbosa* subsp. *subgibbosa* var. *castanea*	*E. subgibbosa* subsp. *subgibbosa* var. *castanea*	*E. subgibbosa*	*E. subgibbosa*	*N. castanea*
N. clavata	*Eriosyce subgibbosa* subsp. *clavata*	*E. subgibbosa* subsp. *clavata*	*E. subgibbosa* subsp. *clavata*	*E. clavata* subsp. *clavata*	*N. clavata*
N. clavata var. *nigrihorrida*	*E. subgibbosa.* subsp. *nigrihorrida*	*E. subgibbosa* subsp. *nigrihorrida*	*E. subgibbosa*	*E. clavata* subsp. *nigrihorrida*	*N. clavata*
N. wagenknechtii var. vallenarensis	*E. subgibbosa* subsp. *vallenarensis*	*E. subgibbosa* subsp. *vallenarensis*	*E. subgibbosa* subsp. *vallenarensis*	close to *E. villosa* (taxonomic rank undecided)	*N. clavata*

N. wagenknechtii var. *wagenknechtii*	*E. subgibbosa* subsp. *wagenknechtii*	*E. subgibbosa* subsp. *wagenknechtii*	*E. subgibbosa* subsp. *wagenknechtii*	close to *E. villosa* (taxonomic rank undecided)	*N. clavata*
N. villosa	*E. villosa*	*E. villosa*	*E. villosa*	*E. villosa*	*N. villosa*
Pyrrhocactus* *group	**Subsect. *Horridocactus***	**Subgen. *Horridocactus* (provisionally)**	***Subgroup Horridocactus***	**Horridocactus group**	***Pyrrhocactus***
N. curvispina var. *curvispina*	*E. curvispina* var. *curvispina*	*E. curvispina* subsp. *curvispina*	*E. curvispina* subsp. *curvispina*	*E. curvispina* subsp. *curvispina*	*P. curvispinus*
N. paucicostata	*E. taltalensis* subsp. *paucicostata*	*E. paucicostata* subsp. *paucicostata*	*E. paucicostata* subsp. *paucicostata*		*P. paucicostatus*
	E. taltalensis subsp. *taltalensis* var. *taltalensis*	*E. taltalensis* subsp. *taltalensis*	*E. taltalensis* subsp. *taltalensis*	*E. taltalensis* subsp. *taltalensis* (close to *Neoporteria*)	
	E. taltalensis subsp. *taltalensis* var. *pygmaea*	*E. taltalensis* subsp. *pygmaea*			
	E. taltalensis subsp. *pilispina*	*E. taltalensis* subsp. *pilispina*	*E. taltalensis* subsp. *pygmaea*		
N. taltalensis var. taltalensis					*P. taltalensis*
N. chilensis		*E. chilensis*		undecided	*P. chilensis*
	E. odieri subsp. *odieri* var. *odieri*				
Thelocephala **group**	**Subsect. *Chileosyce***	**Subgen. *Thelocephala* (provisionally)**	**Subgroup *Thelocephala***	**Subgen. *Chileonapina***	***Thelocephala***
N. odieri var. *odieri*		*E. odieri* subsp.	*E. odieri* subsp.	*E. odieri* subsp. *odieri*	*T. odieri*

		odieri	*odieri*		
N. odieri var. krausii	*E. krausii*	*E. odieri* subsp. *krausii*	*E. odieri* subsp. *krausii*	*E. odieri* subsp. *krausii*	*T. krausii*
Islaya *group*	**Subsect. *Islaya***	**Subgen. *Islaya***	**Subgroup *Islaya***		***Islaya***
N. krainziana	*E. islayensis*	*E. islayensis*	*E. islayensis* subsp. *islayensis*		
Eriosyce	**Subsect. *Eriosyce***	**Subgen. *Eriosyce***	**Subgroup *Eriosyce***		***Eriosyce***
E. sandillon	*E. aurata*	*E. aurata*	*E. aurata*		*E. aurata*

Appendix III.2 Matrix used in morphology based analysis. Asterisk indicates rooting taxon.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38
E_chilensis	0	1	1	2	1	1	2	0	1	1	1	0	0	0	1	1	0	0	1	0	2	1	1	1	2	1	1	0	1	2	0	2	0	0	0	3	2	2
E_senilis_coi	1	2	1	2	1	2	0	0	1	3	3	1	1	1	0	0	1	0	1	1	2	0	2	0	2	1	1	1	1	2	0	2	1	1	1	3	1	1
E_senilis_sen	2	2	0	2	0	3	1	2	1	3	3	2	1	1	0	0	1	0	1	1	2	0	2	0	2	1	1	1	0	2	0	2	0	0	0	3	1	1
E_sociabilis	1	2	0	2	0	1	0	0	1	2	2	2	2	2	2	0	2	0	1	1	2	1	1	1	1	2	1	?	?	?	?	?	?	?	0	2	0	2
E_subgibbosa_cla	1	1	0	0	1	2	0	1	1	3	2	1	1	2	2	0	1	0	1	0	1	1	2	0	2	1	1	2	0	1	1	1	0	0	1	3	2	1
E_subgibbosa_lit	0	2	1	2	0	1	2	2	1	2	2	2	1	2	2	0	0	0	1	2	1	1	2	0	1	1	1	?	?	?	?	?	?	?	0	3	2	0
E_subgibbosa_nig	1	1	0	1	1	2	0	0	1	2	2	1	1	2	2	0	1	0	1	1	2	1	2	0	2	1	1	?	?	?	?	?	?	?	1	3	1	2
E_subgibbosa_val	2	2	0	0	1	1	0	1	1	2	2	1	2	2	2	0	0	0	1	1	1	1	2	0	1	1	1	?	?	?	?	?	?	?	1	3	1	1
E_subgibbosa_wag	0	2	1	0	1	1	0	0	1	2	2	1	2	2	2	0	1	0	2	2	1	1	2	0	0	1	1	?	?	?	?	?	?	?	0	3	2	1
E_sugibbosa_cas	0	1	1	1	1	1	0	1	1	2	3	1	1	1	0	0	1	0	2	1	2	1	2	0	2	1	1	?	?	?	?	?	?	?	0	3	1	1
E_sugibbosa_sub	0	0	1	2	1	1	0	0	1	2	3	1	1	1	0	0	0	0	2	1	2	1	2	0	2	1	1	0	0	2	0	2	0	1	0	3	2	?
E_tal_tal	1	2	0	1	0	1	0	0	0	2	2	2	1	2	2	0	2	0	1	1	2	1	0	2	0	2	1	0	0	2	1	2	0	1	1	1	0	1
E_tal_pil	2	3	0	0	2	3	0	2	0	1	2	2	0	0	1	1	0	0	1	2	1	1	0	2	1	0	0	?	?	?	?	?	?	?	?	1	0	2
E_tal_pyg	2	3	0	0	0	2	0	2	0	1	2	2	0	0	1	1	2	0	1	2	1	1	0	2	1	0	0	1	1	?	0	?	0	0	1	0	0	2
E_villosa	2	2	0	1	0	1	1	2	1	2	2	1	2	2	2	0	2	0	1	2	1	0	2	0	1	1	1	0	0	2	0	2	0	0	0	3	2	1
E_aurata	0	1	1	0	1	2	0	1	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0	2	1	0	0	2	1	0	1	0	2	2	2	0	0	1
E_curvispina_cur	0	2	1	0	1	2	0	1	0	0	1	0	0	0	1	1	1	0	1	1	1	1	0	2	2	3	0	1	1	2	0	2	1	1	2	0	0	1
E_odieri_odi	2	3	0	0	3	4	2	0	0	1	2	2	0	0	1	1	2	1	0	2	2	1	0	2	2	0	0	3	0	1	1	1	0	1	?	0	1	2
E_krausii	2	3	0	0	3	4	0	0	0	1	2	2	0	0	1	1	1	1	0	2	1	2	0	2	2	0	0	2	0	1	0	1	0	1	0	?	0	2
E_islayensis	0	1	0	0	1	0	0	0	0	0	1	2	0	0	1	1	0	1	0	2	0	0	0	2	2	0	0	1	2	1	3	2	0	2	2	0	0	1
C_brevistylus*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	2	0	0	0	1	2	0	3	2	2	2	1	1	0	0

CHAPTER IV: PHYLOGENETIC NICHE DYNAMICS AND THE SPECIATION PROCESS IN *ERIOSYCE* SUBGEN *NEOPORTERIA* (CACTACEAE) UNDER CLIMATIC GRADIENTS AT MEDITERRANEAN CHILE.

IV.1 ABSTRACT

Phylogenetic climatic niche (PCN) dynamics is a clade property related to the divergence process that occurs in areas with climatic changes and gradients. In this study, we characterized and evaluated the role of PCN dynamics in the allopatric divergence of *Eriosyce* subgen. *Neoporteria* (Cactaceae) (hereafter, *Neoporteria*), an endemic group to mediterranean Chile. Also, we evaluated the similarity patterns of seed germination response to temperature and substrate water potential, in order to evaluate the similarity in the germinative fundamental niche of taxa. The PCN of *Neoporteria* varied along time, the pattern of divergence fit the expectation of evolutionary changes tending to climatic optimums (Ornstein–Uhlenbeck model). Indeed, significant differences in the climatic niche and biotope of sister taxa and their intermediate absences indicated that taxonomic divergence is linked to the increase of disparification between taxa. Germination responses of taxa to temperature and substrate water potential suggest that the fundamental germinative niche change among species, but between relative taxa remains invariant. This niche conservatism in early life cycle of plant might be a relevant aspect of the initial separation of population after a climate change, while climatic niche evolution might be related to posterior further divergence between sister taxa.

KEY WORDS: Substrate water potential, Grinnellian niche, geographic isolation, climate change, climatic gradients, hotspot.

IV. 2 INTRODUCTION

Understanding the origin of species is one of the dominant research programs in evolutionary biology (Coyne and Orr 2004). In this sense, geographic isolation of populations is a key mechanism that may drive evolutionary divergence of taxa (Mayr 1947; Barraclough and Vogler. 2000). Among the several ecological factors that can produce the split of the geographic range of an ancestral taxon, climate is thought to be a major force that can favors isolation (Wiens 2004ab; Hua and Wiens 2010). In this sense, climatic changes and oscillations can affect diversification (speciation), and therefore species richness patterns (Stevens 1989; 1992; Willig *et al.* 2003; Wiens 2004a; Kozak and Wiens 2007; Rahbek *et al.* 2007; Kozak and Wiens 2010b). The isolation caused by climatic patterns (environmental gradients and heterogeneity) can be particularly important in arid and semi arid areas, where such variables as precipitation and temperature are critical (Stebbins 1952; Axelrod 1967; Evans *et al.* 2009). In a dynamic climatic scenario with wet-arid phases (such as glaciations oscillations), when one arid phase become prevalent populations may remain in refuges with suitable climatic conditions (Stebbins 1952; Axelrod 1967; Wiens 2004; Evans *et al.* 2009). The persistence of species across space will depend on the geographic availability of suitable climatic conditions where species can survive and maintain positive population rates (Wiens 2004b; Holt 2009), and / or the ability of species to evolve physiological tolerance to the new climatic configuration (Pearman *et al.* 2008).

Divergence mechanisms related with climatic changes are conceptually linked with the duality between the "Grinnellian" niche (climatic domain) and its projection onto physical space called "biotope" (*i.e.* the spatial extension of niche) (Hutchinson 1957; 1959; Soberón 2007; Colwell and Rangel 2009). Exactly, the same *n* environmental attributes defined in the species niche can be projected and mapped, allowing reciprocal projections between the geographic environmental conditions along space and its niche. Consequently, this framework contributes to understand allopatric divergence process unifying the multivariate model of climatic conditions where a species persists in nature, and the geographic model of climatic suitability (Colwell and Rangel 2009). Large conceptual discussion of niche has been realized with the advent of large amount of species distributions information and tools for model the niche and the biotope (Guisan and Thuiller 2005; Kearny 2006; Araújo and Guisan 2006; Soberón 2007; Kozak et al. 2008; Colwell and Rangel 2009). When ecological niche models (ENMs, hereafter) utilize only *scenopoetic* variables (i.e. environmental conditions for which competition is not relevant) to project suitability of specie along the space they indeed represent the biotope (Hutchinson 1978; Colwell and Rangel 2009), the advantages of analyzing the Grinnellian domain of the niche–biotope duality are that these niche requirements may change (evolve) long time and is particularly relevant at biogeographic scales (Soberón 2007).

There are two general models for speciation within the context of niche theory: niche conservatism (or “stasis”) and niche divergence (or “shifts”) (Pearman *et al.* 2008). Niche conservatism is the maintenance of ecological similarity among species or populations over time (Harvey and Pagel 1991, Peterson *et al.* 1999; Prinzing et al. 2001; Wiens and Graham 2005; Wiens et al. 2010b). Niche conservatism of climatic requirements may be an important factor in allopatric speciation, since it may be the initial cause of geographic isolation between two incipient species (Wiens 2004ab; Kozak and Wiens 2006; Hua and Wiens 2010). A species may be split into two allopatric descendant species when suboptimal climatic conditions for the species divides the climatic biotope of the ancestral species, and niche conservatism constraints the expansion of the biotope into the intermediate areas, thus preventing gene flow between them (Wiens 2004a; Hua and Wiens 2010). This model predicts that recently evolved taxa will have equivalent biotopes and climatic niches, and the intermediate area will be climatically unsuitable for both species (Fig 1a).

Niche divergence is a classic speciation mechanism that indicates that new species originates by means the expansion of the ancestral species niche, thus covering new conditions (Losos *et al.* 2003; Pearman *et al.* 2008). Under this model it is expected that the climatic biotope between sister taxa split following niche divergence (Pearman *et al.* 2008). This interspecific disparity of niche is also called "disparification" and may be linked to the diversification of a clade (Evans *et al.* 2009). Under both model of niche dynamics, the climatic characteristics of intermediate absences can highlight additional details in the divergence process (Kozak and Wiens 2006; Hua and Wiens 2010). When the climatic niche and biotope are different between sister taxa, but are more similar to each other than the area that separate them, constitute indirect evidence suggesting that the initial allopatry was established after a climate change by niche conservatism, and subsequently diverge ecologically from their ancestral species' niche in allopatry limiting any further gene flow between them (Hua and Wiens 2010). Also, the intermediate absences can be more similar to each taxa than they are between them, in such cases niche evolution might prevent posterior gene interchange between sister taxa (Fig 1d). Finally when taxa conserve their climatic niches and the areas of climatic suitability (biotope) occur along the distribution of taxa and intermediate areas, is a clear indicative that climatic similarity may not be relevant for divergence of taxa.

The climatic niche is the basis of the "persistence" niche (i.e. conditions that enables a positive demographic tendency in a population or specie) (Holt 2009). An interesting relationship between the climatic and the "establishment" or "regeneration" niche (*sensu* Grubb 1977) can reveal patterns of coupled or uncoupled ecological dynamics between both (Holt 2009). The germination niche is the configuration of abiotic requirements needed for seed germination, also is a relevant component of the "regeneration" niche which in turn influences population dynamics in plants (Grubb 1977; Harper 1977). Comparisons between the climatic and germinative niches in allopatric species may highlight the evolutionary process involved in the geographic divergence between sister taxa. A coupled evolutionary tendencies in both niche domains suggest stability between persistence and establishment environmental conditions, while uncoupled dynamics might suggest distinct demographic performance along a climatic gradient (Holt 2009). For example, evolutionary change in the germinative and climatic niches may indicate that species experienced local adaptation (evolution of climatic tolerances) along a climatic gradient; this also suggest that the evolutionary change in niche domains may constraints gene flow between sister taxa (Table 1). In contrast, conservatisms in both germinative and climatic niches indicate niche stasis, and that ecological restrictions prevent niche evolution and gene flow in a landscape with climatic patches (not gradients). Some interesting intermediate situations can also occur, such as shift in germinative niche but conservatism in climatic niche suggesting selective pressure in the seed–seedlings stages but relaxed selection in adults. This fact suggests that the divergence between sister taxa by micro evolutionary process favored differential safe sites es for germination (Harper 1977). For the contrary, conservatism in germinative niche but shift in climatic niche may be a signal of soft selection in early stages or physiological restrictions compared to subsequent ontogenetic stages (Table 1). If it so, then environmental conditions for persistence and regeneration is uncoupled, and that the demographic performance along a climatic gradient particularly in marginal populations will be severely constrained favoring isolation (Holt 2009).

Mediterranean central Chile is a world biodiversity hotspot since the high levels of endemisms of animal and plants are similar to the percentages observed in some oceanic islands (Myers *et al.* 2000). North and central Chile have one of the most notable latitudinal climatic gradient of the world, with an annual mean rainfall ranging from virtually zero at the north of 25°S along the Atacama desert to about 1.100 mm at 36°S (Houston and Hartley 2003; Garreaud *et al.* 2008). Also the long seismic and volcanic history generated a complex topography of central Chile, that includes the Andes and Coastal ranges, transversal (longitudinal) mountain chains and valleys produce, thus producing a drastic elevational gradient. Further, this area experienced changes in precipitations during the Pliocene and Pleistocene with wet - dry periods (Villagrán 1994; Wara *et al.* 2005; Maldonado and Villagrán 2006; Placzek *et al.* 2009).

The evolutionary diversification of Cactaceae has been of great interest in the evolutionary biology of plants, with more than 100 genus and 1,500 species is one of the most conspicuous and diverse Angiosperm families in the Neotropic (Hershkovitz and Zimmer 1997; Anderson 2001; Hunt *et al.* 2006). As a consequence of its remarkable diversity, Cactaceae is an appropriate group for study species divergence and the mechanisms involved in this processes. The endemism and species richness of Chilean cacti is one of the highest within the Chilean angiosperm families (Marticorena 1990; Ortega-Baes and Godínez-Alvarez. 2006; Guerrero et al. 2011a).

In this study we focused on *Eriosyce* subgen. *Neoporteria* (Britton & Rose) Helmut Walter (*Neoporteria,* hereafter) a group of Cactaceae that has a peak of taxonomic richness in the climatic transition between arid and semi–arid environment of Chile, and are principally allopatric distributed along the latitudinal and altitudinal gradients (see Chapter 3). More specifically, we focused on the effects of climatic change and gradients on the evolutionary disparity of niche and diversification of *Neoporteria*. We hypothesized an niche disparity (climatic and germinative) and spatial segregation of climatic biotopes among sister taxa as a consequence of local adaptation to distinct climatic configurations. To do this we conducted quantitative analyses to evaluate the phylogenetic climatic niche dynamics and the role of historic climatic changes in the current divergence process in *Neoporteria.* Also, we examined the configuration of spatial climatic suitability of sister taxa using ecological niche models to determined geographic isolation between sister taxa. Finally, we compared similarity patterns of the germinative fundamental niche, in order to evaluate coupled patterns between germinative and climatic niches.

IV.3 MATERIALS AND METHODS

Phylogenetic niche dynamics

A previous study showed that 11 taxa of *Neoporteria* form a monophyletic group (Chapter 2). We utilized Bayesian phylogenetic reconstruction based on combined molecular dataset of two chloroplast zones (*rpl32–trnL* and *trnL–trnF*) (see Chapter 2 for DNA extractions and amplification protocols, Genbank codes and phylogenetic methods).

In this study we considered "the climatic niche" of a species as a set of vectors characterized by bioclimatic variables constructed for each locality of species. To evaluate phylogenetic niche dynamics, firstly we obtained the climatic data from each taxon using GIS–based environmental layer from georeferenced specimens' localities and populations (for details see Guerrero *et al.* 2011a). We extracted climatic variables for each presence from the WORLDCLIM database with 1 km^2 spatial resolution (Hijmans et al. 2005); these variables describe temperature and precipitation for all the occurrence localities along *Eriosyce* subgen. *Neoporteria* geographic range (more details of occurrence data are available in Guerrero *et al.* 2011a). To account for the potential redundancy among the 19 bioclimatic variables and to reduce the number of variables, we performed a principal component analysis (PCA) for the complete matrix (19 variables with all species localities). The phylogenetic dynamics of the climatic niche was evaluated considering the two first canonical axes that accounted for the 74% of the total variance. For both axes we evaluated their disparity along time (Harmon et al. 2008), this analysis provides a running average disparity for clades of a given age range through the history of the tree compared to the expectation under a null model of Brownian Motion. Relative disparity plots quantify the distribution of disparity within versus among subclades, and may be considered a measure of niche evolution versus conservatism. We calculated morphological disparity index (MDI: Harmon et al. 2003) which compares observed disparity to that expected under Brownian motion model of evolution, negative values of MDI indicate that disparity tend to be distributed among subclades (because of niche evolution among subclades and conservatism within subclades), whereas positive values of MDI indicate that disparity tends to be distributed within subclades (because niche evolution within subclades) (Evans et al. 2009).

In addition we projected the phylogeny of *Eriosyce* subgen. *Neoporteria* into a multivariate climatic space (hereafter, a "phyloclimaticspace"), this method is useful to map the history of the diversification of climatic requirements and infer the magnitude and direction of change along any branch of the phylogeny (Sidlauskas 2008). Specifically, phyloclimaticspace characterized by a short branches indicates low levels of diversification of climatic requirements along the evolutionary time, whereas a phyloclimaticspace with long branches and large separation between relatives taxa indicates change of climatic requirements. Finally we evaluated the divergence patterns analyzing the evolution models Brownian Motion (BM) and Ornstein–Uhlenbeck (OU) (Kozak and Wiens 2010ab) of climatic requirements. All these analyses were run using the packages GEIGER, OUCH and APE and the function Phylomorphospace v0.3 (Revell 2011) available in R (http://www.R–project.org).

Identification of sister taxa

Using the Bayesian phylogenetic tree we identified three pairs of sister and one sister group composed by three taxa (Fig. 2). We decide to not include the *E. chilensis – E. subgibbosa* var. *litoralis* pair because we suspect that this former species might have a reticular origin (Chapter 2). The allopatric sister taxa groups analyzed in this study were:

(I) *E. senilis* subsp. *senilis* (Backeb.) Katt. [acronym: *E_senilis_sen*] – subsp. *coimasensis* (F. Ritter) Katt. [acronym: *E_senilis_coi*].

(II) *E. subgibbosa* subsp. *clavata* (Söhrens ex K. Schum.) Katt. [acronym: *E_subgibbosa_cla*] – subsp. *nigrihorrida* (Backeb. ex A.W.Hill) Katt. [acronym: *E_subgibbosa_nig*].

(III) *E. subgibbosa* var. *subgibbosa* (Haw.) Katt. [acronym: *E_subgibbosa_sub*].– var. *castanea* (F. Ritter) Katt. [acronym: *E_subgibbosa_cas*]
(IV) *E. subgibbosa* subsp. *vallenarensis* (F. Ritter) Katt. [acronym: *E_subgibbosa_val*] – *E. subgibbosa* subsp. *wagenknechtii* (F. Ritter) Katt. [acronym: *E_subgibbosa_wag*] – *E. villosa* (Monv.) Katt. [acronym: *E_villosa*]

Climatic niche of sister taxa

To test whether historic climate changes causes populations become isolated we characterized the climatic conditions of the geographic spaces between sister taxa. In order to do that, we randomly generated pseudo-absence locations between the closest presence localities among sister taxa. The number of pseudo-absence localities was equal to the average of the number sampling localities for sister taxa. We extracted climatic variables for each presence and absence localities from the WORLDCLIM database with 1 km^2 spatial resolution (Hijmans et al. 2005).

To calculate the climatic distances among sister taxa and the space between sister taxa (= pseudo-absences), we first run a principal component analysis (PCA) to account for the possible redundancy among the 19 variables for each sister taxa and their corresponding absence locations. Afterwards we calculated Fisher and Mahalanobis distances (F_d and M_d) using the PCs that account for at least 95% of the variance, in our comparisons the first 3–4 PCs that satisfied this condition. To test whether climatic distances were significantly different between the climatic niche of sister taxa and their intermediate absences, we calculate the p value of Fisher distances. These analyses were performed using XLSTAT version 2011 (Addinsoft, Brooklyn, NY, USA).

Climatic biotope of sister taxa

To test whether niche dynamics causes populations isolation, we analyzed the biotope of sister taxa, and the climatic suitability of intermediate areas. Particularly, "biotope" is defined here as a "set of grid cells in geographic space, defined by actual or potential ways in which presences of individuals of a species are predicted to occur given a certain niche".

Although, the biotope and the climatic suitability of intermediate areas are essentially estimated using the same procedure (using ENMs) we named them differentially because the biotope is related to the niche of taxa, while climatic suitability is related to the climatic configuration of pseudo-absences. The climatic biotope of taxa was constructed utilizing Maxent version 3.3.3e (Phillips et al. 2006). Maxent and other techniques that calculate climatic suitability along the geography are generally named "ecological niche modeling" or "predictive distribution models", under the niche–biotope duality framework we will consider it as the biotope model since it is the geographic projection of the climatic niche.

We run two set of preliminar analyses to choose whether utilize models constructed with the 19–bioclimatic dataset, or models based on environmental layers that consisted on the first four principal components resulting from a PCA which included the 19–bioclimatic layers. Both models were replicated at least 100 times, and then were compared them using Bayesian (BIC), and sample size corrected Akaike information criteria (AICc) (Warren and Seifert 2011). The best model always was one in which we used the 19-bioclimatic variables. Afterward, we evaluated the similarity patterns between the sister taxa biotopes, and between the biotope of each sister taxa and the climatic suitability of intermediate areas. These statistics are based on *I* or Schoener's *D* statistics and summarize the similarity of projected suitability scores for each 1–km^2 grid cell of a shared landscape and range from 0 (ENMs highly divergent) to 1 (ENMs identical) (Warren et al. 2008; Glor and Warren 2011). However, *D* values must be interpreted with caution because this metric assume that different occurrence probabilities are proportional to local species densities or other measure of relative use (Warren *et al.* 2008). In contrast, the metric "*I*" was developed to avoid that assumptions (Warren *et al.* 2008).

Germinative niche

To evaluate the germinative niche of species we conducted experimental "common garden" germination essays using germination chambers. Seeds were collected between October and December 2009 in natural populations extracted from mature fruits, in at least 10 individuals per species. Fruits are mature when they are easily extracted from the mother plant and seeds fall off from the basal abscission. Seeds were collected in the same populations used for DNA extractions (Chapter 2). We pooled the seeds in a single paper bag per species and maintained them in dry conditions until the experiment started in April 2010.

We evaluated seed germination at different temperature and water stress, both variables are considered crucial for the germination process in plants. Given that seeds of *Neoporteria* taxa are positive photoblastic we did not considered light into this study (Guerrero *et al.* 2011b). Particularly, we produced three night–day temperatures in separate essays: (a) 4–9°C, (b) 11–15°C and (c) 16–21°C with a photoperiod of 12/12 hrs. These temperatures regimes were chosen from the minimum (night) and maximum (day) temperatures estimated at the occurrences sites of all taxa, and then, we calculated the mean values of the minimum temperature, mean temperature and maximum temperatures during a typical wet season (autumn and winter) in central Chile. Water potentials was modified using a range of Mannitol concentrations diluted in deionized water (0, 0.1, 0.2, 0.4, 0.6 mol/L), to generate substrate water potentials of 0, –0.25, –0.5, –1, and –1.5 Mpa. The effects of solutes upon water potentials (Ψ) was calculated based on the expression:

$$\Psi = -RTC_s,$$

where R is the ideal gas constant, T the absolute temperature, and C_s the osmolarity of the Mannitol solution (Taiz and Zeiger 1991; Swagel *et al.* 1997). For compound such as Mannitol 1 mol/L solution generates Ψ of –2.5 MPa. For each temperature essay we treated seeds using the complete range of water potentials; however no seed germination was registered with a water potential of –1.5 Mpa.

We sown 10 seeds/taxon in separate enclosed Petri dishes on a substrate of 2 g of vermiculite and placed them in a germination chamber with a photoperiod of 12/12 hrs. Each of the five–substrate water potentials levels was replicated in five Petri dishes in each of the three temperature levels (n = 60 Petri dishes per taxon, a total of 600 seeds). All treatments were watered with deionized water only once at the beginning of the experiment. Once a week, we registered the germinated seeds until no further germination was observed. Seeds were considered to be viable if at the end of the experiment they maintained their hardness and the embryos were white and turgid. All seeds were viable using these criteria.

We used a two–way ANOVA to test the effect of species and water stress in germination. Each temperature essay was analyzed in separate analyses. The proportions of germination were arcsine transformed to fit ANOVA assumptions (Zar, 1999).

IV.4 RESULTS

Phylogenetic niche dynamics

Variation in the climatic niche was detected along the evolutionary time for the *Neoporteria* clade, this pattern was revealed by the principal component analysis, the phyloclimaticspace and the relative disparity along time. Most of bioclimatic variables were correlated with latitude and elevation, indicating that they are associated with climatic gradients (Table 2). The first two PCs explained >70% of the variation among taxa, PC1 have strongest factor loadings associated to precipitations variables and is correlated with latitude as well (factor loadings >

±0.9: annual precipitation, precipitation of the wettest month, precipitation of the driest month and precipitation of the coldest quarter), the PC2 give more weight to temperature variables and is also correlated with elevation (factor loadings > ± 0.9: mean temperature of the driest quarter; BIO10 = mean temperature of the warmest quarter) (Table 2).

The PCA showed that the *Neoporteria* clade occupied extensive amplitude of the climatic–niche space (Fig. 3ab), it also showed that each taxon occurred in distinct regions of the current climatic space (Fig. 3). The phyloclimaticspace showed a expansion of the climatic space between the ancestral nodes and the current taxonomic configuration (Fig. 3b). Both analysis showed a process of clear divergence between of sister taxa.

Relative disparity along time of first axis suggest that divergence of the PC1 tends to be distributed homogenously among–within the subclades (MDI = 0.020) (Fig. 4a), and did not differ substantially to an unconstrained Brownian motion model of evolution. However, further analyses indicate that divergence patterns tends to vary toward an optimum since the Ornstein–Uhlenbeck model have strongest fit (BM AICc= 4633.559; OU AICc= 62.041). The disparity of PC2 indicates that variation tends to be distributed within subclades (because of niche evolution within subclades) (MDI = 0.708) (Fig. 4b). Similarly to PC1, the pattern of divergence pattern of PC2 tends to vary toward an optimum (BM AICc= 4062.133; OU AICc= 51.988).

Climatic niche of sister taxa

The variation the phylogenetic climatic niche is consistent with the comparisons of sister taxa and the intermediate climatic space. Variation in the multivariate climatic niche is a widespread pattern in *Neoporteria*, even though when quantifying and comparing the first four principal components (> 95% of the variation among taxa) of each sister taxa (Table 3–6). All Fisher distances of climatic configuration between sister taxa and their intermediate areas were significant, except between *E. subgibbosa* var. *castanea* and at intermediate areas (Table 4), suggesting a more recent geographic isolation compare to other *Neoporteria* disyunctions.

Climatic biotope of sister taxa

Similarity analyses of the climatic biotopes showed that they are substantially segregated between sisters taxa (*I:* <0.5; Table 7-10). Only two higher *I* values was obtained among comparisons suggesting some level of climatic suitability overlap between *E. subgibbosa* subsp. *clavata* and subsp. *nigrihorrida* (I = 0.610), and *E. subgibbosa* subsp. *vallenarensis*, and *E. villosa* (I = 0.506). Overall, these analyses are evidence that support the spatial separation of sister taxa biotopes.

The similarity between the intermediate areas and sister taxa biotopes, indicated that in most of cases, have different spatial climatic configurations (Tables 7-10); however *I* values showed larger values of similarity compare with *D*. Overall, these analyses showed that intermediate areas have substantial differences of climatic characteristic along the geographic space compare to sister taxa biotopes. However, the similarity metrics (*I* and *D*) indicated that sister taxa are more different between each other than the intermediate areas (Tables 7-10). These results support the existence of climatic gradients between the geographic range of sister taxa.

Germinative fundamental niche

Experiments showed that seed germination varied among taxa and substrate water potential (Ψ) (Fig. 5) at the three temperatures conditions: 4–9°C (taxa: $F_{8, 179}$ = 15.615, $P < 0.0001$; Ψ: $F_{3, 179}$ = 105.167, $P < 0.0001$), 11–15°C (taxa: $F_{8,179}$ = 22.851, $P < 0.0001$; Ψ: $F_{3, 179}$ =137.402, $P < 0.0001$), and 16–21°C (taxa: $F_{8, 179}$= 20.142, $P < 0.0001$; Ψ: $F_{3, 179}$ = 104.532, $P < 0.0001$). Theses analyses suggest a wide range of seed responses to environmental variation in the *Neoporteria* clade.

Also, in the three temperatures we detected significant interactions between taxa responded and substrate water potential (4–9°C: $F_{24, 179} = 6.327$, $P < 0.0001$; 11–15°C: $F_{24, 179} = 1.990$, $P = 0.007$; 16–21°C: $F_{24, 179} = 2.413$, $P < 0.0001$). These analyses suggest that the seeds of taxa germinated differentially under dissimilar substrate water potentials, and therefore in general terms taxa have different germination niches. However, more specific analyses indicated that sister taxa tend to germinate equivalently in the same water substrate water levels in the three temperatures conditions (Table 11), suggesting germinative niche conservatism between sister taxa.

IV. 5 DISCUSSION

In this study, we evaluated the phylogenetic niche dynamics and examined its role in the divergence processes of the endemic and diverse group *Neoporteria*, under climatic gradients of central mediterranean Chile. Our results support the variation of climatic niche and biotope as key factors in the ongoing diversification processes. Also, we found that in general the germinative fundamental niche varied across taxa, while sister taxa have equivalent germination patterns. Niche conservatism in germination may highlight how marginal populations can easy experience demographic bottlenecks after climate changes. The relationship between phylogenetic relatedness and ecological niche similarity among species has been investigated profusely the last two decades (Losos 2008; Wiens et al. 2010). Different patterns of phylogenetic signal and phylogenetic niche conservatism have been documented since new comparative methods have been developed and new systematic data are now available (Graham *et al.* 2004; Losos 2008, Kozak et al. 2008; Wiens et al. 2010). In this study we detected that climatic niche substantially varied along the evolutionary time (Fig 3-4), and that disparification pattern of the climatic niche tend to change towards an optima across different taxa (i.e. Ornstein–Uhlenbeck model). Further, the phylogenetic niche dynamic of *Neoporteria* indicates evolutionary change varying within and among subclades (Fig. 4). These dynamic tendencies of climatic niche suggest an evolutionary history of *Neoporteria* linked to climatic changes, and influenced by current climatic gradient.

Beyond the phylogenetic patterns of niche, the interest to study niche dynamics as part of different macro-evolutionary processes has gained a growing interest (Losos 2008; Wiens *et al.* 2010). Here, we showed that differences in the niche of sister taxa are related with their allopatric divergence, as disjunct distributions of climatic suitability (biotopes) favors isolation (Raxworthy *et al.* 2007). These results are also supported by the different climatic conditions that prevail in the intermediate areas, therefore contribute to constraint regeneration and dispersal between populations (Kozak and Wiens 2010a). Cleary, climatic gradients impose a restrictive scenario for the geographic spread of populations' ranges, and even after subtle climate changes marginal populations can reduce demographic parameters because they are located at suboptimal zones of the climatic niche (Holt 2009).

In Atacama and mediterranean Chile elevational gradients are related with species richness and the extent of geographic range of endemic cacti (Guerrero *et al.* 2011a); at low taxonomic levels, *Neoporteria* diversification might be the result of combined effects of climatic gradients that varied with elevation and latitude. The relative importance of climatic niche divergence supports the evolutionary change in climatic tolerances along climatic and geographic gradients. As expected, climatic niche disparification induce low similarity in the climatic biotopes of sister taxa. The differences of climatic configuration along gradients are also showed by the similarity analyses highlighting that intermediate areas are more similar to sister taxa than this last with each other (Fig. 1b).

Climatic biotopes and phylogenetic niche dynamics suggests that sister taxa ancestors extended widely along the geographic gradient, and that the split into new allopatric taxa was caused by climatic changes. In fact, the increase in aridity that occurred during the Pliocene initiated the diversification of other plant group such as *Nolana* (Dillon *et al.* 2009), *Prosopis* (Catalano *et al.,* 2008), *Astragalus* (Scherson *et al.* 2008), and *Palaua* (Huertas *et al.* 2007). Furthermore the dominant arid climate was interrumped by short wet periods during the Pleistocene affecting plant distributions along Atacama and mediterranean Chile (Lamy *et al.* 2001; Maldonado *et al.* 2005; Wara *et al.* 2005; Maldonado and Villagrán 2006; Nester *et al.* 2007; Placzek *et al.* 2009). The influence of climatic variability into biodiversity has been important (Samaniego and Marquet 2009), affecting distribution patterns of vegetation (Villagrán 1994; Maldonado and Villagrán 2006; Placzek *et al.* 2009), genetic structure of populations (Bull-Hereñu *et al.* 2005) and Cactaceae richness patterns (Guerrero *et al.* 2011a). Current climatic conditions of coastal north-central Chile resembles to a large-scale decadal "La Niña phase" with ongoing reductions in precipitations and temperatures between 17°-37°S (Falvey and Garreaud 2009); these current conditions suggests that the actual phase is favoring the isolation between populations. Also, climatic gradients currently are intensifying because the increasing contrasts between the coastal cooling and the warming conditions in the central valley and Andes of central and northern Chile (Falvey and Garreaud 2009).

In Figure 6, we illustrated the hypothetical diversification process of the *Neoporteria* clade in relation to wet-dry periods. Sister taxa (same color and roman number) are encircled by large ellipses that represent their combined biotope, and may be associated to the geographic range of the ancestor when climate was more suitable with more gently gradients. The current biotope (dashed black lines) of sister taxa are now segregated and allopatry is favoring their evolutionary divergence (Fig. 6). The magnitude of climatic gradients after aridization and niche dynamics will determinate if taxa can persist in both areas or will become locally extinct. This example supposes climatic niche change, as biotopes are spatially isolated in the geographic space niche, but also assumes some level of conservatism because taxa failed to establish in intermediate areas.

Analyses of species' niches are essential to understanding controls on species' geographical range limits and how these limits might shift in a region with climatic changes (Holt 2009). The germinative niche is a crucial aspect in plant "regeneration" or "establishment" niche because it might influence the demographic fate of plants (Grubb 1977; Harper 1977). Our experimental common garden essays that evaluated seed germination responses to a range on abiotic conditions, revealed some levels of niche conservatism in the fundamental germination niche because although seed germination varied among taxa (Fig. 5), sister taxa responded equivalently in most of cases (Table 3). The role of conservatism of germinative fundamental niche in initiating geographic isolation might be crucial, since germination process is a key process in population dynamics of plants (Harper 1977). The uncoupled evolutionary tendencies of the divergent climatic (persistence) and conservative germination (establishment) niche suggest that climate change induce the increase in the climatic niche disparity, however physiological constraints restrict this change in their germinative niche favoring the extinction of marginal populations (Holt 2009).

Clearly, the evolution of *Neoporteria* is complex and is the result of the interplay between abiotic and biotic factors (Guerrero et al. 2011c); overall this study show high climatic disparity of climatic niche, segregated climatic biotopes and conservatism in germination, which suggest a straightforward relationship between the ongoing geographic speciation process in *Neoporteria* and the effects of environmental gradients derived from historical climate changes occurred at north and central Chile.

Table IV.1 Evolutionary interpretation of different scenarios of shift and conservatism in the germinative and climatic niches.

		Climatic niche	
		Divergence	**Conservatism**
Germinative niche	**Divergence**	Niche evolution.	Selective pressure in early stages.
	Conservatism	Niche conservatism in early stages, followed by ontogenetic niche change.	Niche conservatism.

Table IV.2 Factor loadings and eigenvalues from the principal components analysis of the 19-bioclimatic variables. PC1–PC4 explained > 95% of the variation among taxa. Factor loadings > ±0.9 are highlighted using bold letters. Asterisks and crosses indicate variables that are correlated ($P \leq 0.05$) with elevation and / or latitude, respectively. Degrees of freedom of correlations were spatially corrected (Rangel et al. 2010).

Variable	PC1†	PC2*	PC3*	PC4
bio1*	–0.574	0.795	–0.170	0.083
bio2*	0.549	0.287	0.743	0.241
bio3*	–0.173	–0.296	0.382	0.855
bio4	0.677	0.498	0.485	–0.233
bio5	0.320	0.877	0.350	0.048
bio6*	–0.689	0.347	–0.626	0.084
bio7*	0.656	0.401	0.638	–0.018
bio8*	–0.748	0.481	–0.400	0.197
bio9*	–0.232	**0.967**	0.013	–0.022
bio10*†	–0.187	**0.978**	0.061	–0.050
bio11*	–0.797	0.441	–0.375	0.162
bio12†	**0.916**	0.141	–0.326	0.107
bio13†	**0.906**	0.135	–0.295	0.117
bio14	0.832	0.085	–0.380	–0.006
bio15	–0.711	–0.075	0.249	–0.111
bio16†	**0.912**	0.144	–0.312	0.110
bio17	0.873	0.061	–0.392	0.025
bio18	0.875	0.048	–0.400	0.028
bio19†	**0.909**	0.135	–0.305	0.123
Eigenvalue	9.454	4.515	3.091	0.994
% Variation	49.756	23.761	16.268	5.233

Bioclimatic variables are as follows: BIO1 = annual mean temperature; BIO2 = mean diurnal temperature range [mean of monthly (maximum temperature) minimum temperature)]; BIO3 =

isothermality (BIO2 / BIO7 · 100); BIO4 = temperature seasonality (standard deviation of monthly temperature); BIO5 = minimum temperature of the coldest month; BIO6 = maximum temperature of the warmest month; BIO7 = temperature range (BIO6) BIO5); BIO8 = mean temperature of the wettest quarter; BIO9 = mean temperature of the driest quarter; BIO10 = mean temperature of the warmest quarter; BIO11 = mean temperature of the coldest quarter; BIO12 = annual precipitation; BIO13 = precipitation of the wet– test month; BIO14 = precipitation of the driest month; BIO15 = precipitation seasonality (standard deviation of monthly precipitation); BIO16 = precipitation of the wettest quarter; BIO17 = precipitation of the driest quarter; BIO18 = precipitation of the warmest quarter; BIO19 = precipitation of the coldest quarter.

Table IV.3 Fisher (left) and Mahalanobis distances (right) of the climatic configuration between *E. senilis* subsp. *senilis*, subsp. *coimasensis* and their intermediate absences. All Fisher distances are statistically significant (*p*=0.0001)

	Absences	E_senilis_coi	E_senilis_sen
Absences	0 - 0	13.724 - 5.822	19.229 - 6.147
E_senilis_coi		0 - 0	37.738 - 14.199
E_senilis_sen			0 - 0

Table IV.4 Fisher (left) and Mahalanobis distances (right) of the climatic configuration between *E. subgibbosa* var. *subgibbosa*, var. *castanea* and their intermediate absences. All Fisher distances are statistically significant (*p*=0.0001), except indicated by an asterisk (*p*=0.151)

	Absences	E_subgibbosa_cas	E_subgibbosa_sub
Absences	0 - 0	1.834* - 0.903	28.705 - 7.644
E_subgibbosa_cas		0 - 0	32.983 - 12.995
E_subgibbosa_sub			0 - 0

Table IV.5 Fisher (left) and Mahalanobis distances (right) of the climatic configuration between *E. subgibbosa* subsp. *clavata*, subsp. *nigrihorrida* and their intermediate absences. All Fisher distances are statistically significant (*p*=0.0001)

	Absences	E_subgibbosa_cla	E_subgibbosa_nig
Absences	0 - 0	8.373 - 5.127	5.665 - 2.960
E_subgibbosa_cla		0 - 0	21.254 - 13.352
E_subgibbosa_nig			0 - 0

Table IV.6 Fisher (left) and Mahalanobis distances (right) of the climatic configuration between *E. subgibbosa* subsp. *vallenarensis*, subsp. *wagenknechtii, E. villosa* and their intermediate absences. All Fisher distances are statistically significant (*p*=0.0001).

	Absences	E_subgibbosa_val	E_subgibbosa_wag	E_villosa
Absences	0 - 0	14.372 - 3.963	17.417 - 6.083	9.995 - 3.344
E_subgibbosa_val		0 - 0	47.625 - 17.509	25.243 - 8.909
E_subgibbosa_wag			0 - 0	20.690 - 8.824
E_villosa				0 - 0

Table IV.7 Biotope similarity between *E. senilis* subsp. *senilis*, subsp. *coimasensis* and their intermediate absences of projected suitability scores for each 1–km^2 grid cell of a shared landscape. Numbers are *I* (Left) and Schoener's *D* (right), both metrics range from 0 (ENMs highly divergent) to 1 (ENMs identical).

	Absences	E_senilis_coi	E_senilis_sen
Absences	1 - 1	0.554 – 0.266	0.490 – 0.245
E_senilis_coi		1 - 1	0.289 – 0.085
E_senilis_sen			1 - 1

Table IV.8 Biotope similarity between *E. subgibbosa* var. *subgibbosa*, var. *castanea* and their intermediate absences of projected suitability scores for each 1–km^2 grid cell of a shared landscape. Numbers are *I* (Left) and Schoener's *D* (right), both metrics range from 0 (ENMs highly divergent) to 1 (ENMs identical).

	Absences	E_subgibbosa_cas	E_subgibbosa_sub
Absences	1 - 1	0.752 – 0.475	0.569 – 0.303
E_subgibbosa_cas		1 - 1	0.337 – 0.137
E_subgibbosa_sub			1 - 1

Table IV.9 Biotope similarity between *E. subgibbosa* subsp. *clavata*, subsp. *nigrihorrida* and their intermediate absences of projected suitability scores for each 1–km^2 grid cell of a shared landscape. Numbers are *I* (Left) and Schoener's *D* (right), both metrics range from 0 (ENMs highly divergent) to 1 (ENMs identical).

	Absences	E_subgibbosa_cla	E_subgibbosa_nig
Absences	1 - 1	0.632 – 0.396	0.844 – 0.579
E_subgibbosa_cla		1 - 1	0.610 – 0.379
E_subgibbosa_nig			1 - 1

Table IV.10 Biotope similarity between *E. subgibbosa* subsp. *vallenarensis*, subsp. *wagenknechtii, E. villosa* and their intermediate absences of projected suitability scores for each 1–km^2 grid cell of a shared landscape. Numbers are *I* (Left) and Schoener's *D* (right), both metrics range from 0 (ENMs highly divergent) to 1 (ENMs identical).

	Absences	E_subgibbosa_val	E_subgibbosa_wag	E_villosa
Absences	1 - 1	0.423 – 0.235	0.414 – 0.200	0.820 – 0.564
E_subgibbosa_val		1 - 1	0.126 – 0.039	0.506 – 0.301
E_subgibbosa_wag			1 - 1	0.443 – 0.236
E_villosa				1 - 1

Table IV.11 Germination probabilities of *Eriosyce* subgen. *Neoporteria* in three different night–day temperature regimes (night–day: 4–9°C, 11–15°C, 16–21°C). Taxa that are connected with different letters in each temperature level are significantly different based on Tukey test.

		Temperature (night–day)		
Taxa	**Sister taxa**	**4–9°C**	**11–15°C**	**16–21°C**
E_senilis_coi	I	0.00 ± 0.00 ^{c}	0.17 ± 0.04 ^{e}	0.27 ± 0.07 ^{ef}
E_senilis_sen	I	0.00 ± 0.00 ^{c}	0.13 ± 0.03 ^{e}	0.13 ± 0.04 ^{f}
E_subgibbosa_cla	II	0.22 ± 0.07 ^{ab}	0.25 ± 0.05 ^{de}	0.34 ± 0.06 ^{de}
E_ subgibbosa_nig	II	0.10 ± 0.04 ^{bc}	0.35 ± 0.07 ^{cd}	0.31 ± 0.06 ^{de}
E_subgibbosa_cas	III	0.11 ± 0.03 ^{abc}	0.53 ± 0.10 ^{ab}	0.58 ± 0.09 ^{bc}
E_subgibbosa_sub	III	0.22 ± 0.07 ^{ab}	0.54 ± 0.08 ^{a}	0.70 ± 0.08 ^{ab}
E_ subgibbosa_val	IV	0.28 ± 0.07 ^{a}	0.66 ± 0.08 ^{a}	0.58 ± 0.06 ^{bc}
E_subgibbosa_wag	IV	0.10 ± 0.04 ^{bc}	0.44 ± 0.07 ^{bc}	0.45 ± 0.07 ^{cde}
E_villosa	IV	0.14 ± 0.04 ^{ab}	0.45 ± 0.06 ^{bc}	0.50 ± 0.07 ^{bcd}

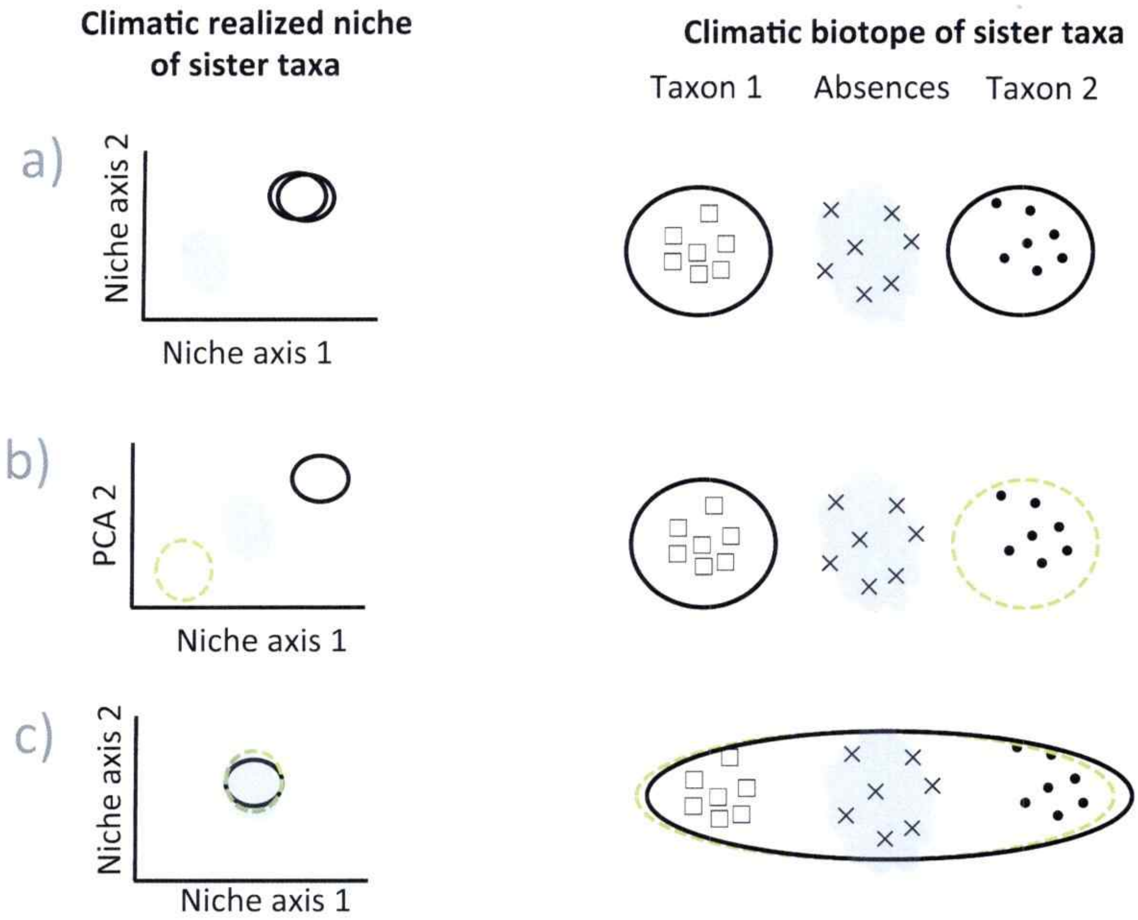

Figure IV.1. Hypothetical examples of the relationship between niche (left) and biotope (right) and their implications for speciation mechanisms. Here, biotope is the geographic representation of the climatic niche and therefore can be inferred using predictive distribution modeling. Absences biotopes correspond to the climatic configuration evaluated using information of absences localities. a) Taxon 1 and taxon 2 have similar climatic niche (conservatism) and the intermediate absences have different climatic configuration, thus both taxa are predicted to occur (due to biotope similarity) in its sister species' geographic range, but not in the intervening gap area; b) Taxon 1 and taxon 2 have diferent climatic niche (niche evolution) and the intermediate have different climatic configuration, as well. Species are not predicted to occur in either its sister species' geographic range or in the intervening gap region; c) Taxon 1 and taxon 2 have similar climatic niche and the intermediate absences have equivalent climatic configuration, as well. Taxon 1 is predicted to occur both in its sister species' geographic range and in the intervening gap between their ranges. This pattern suggests that the current allopatric distributions of sister species are determined by factors other than climate, and so the climatic similarity of species (and similarity to gap locations) may not be relevant to speciation.

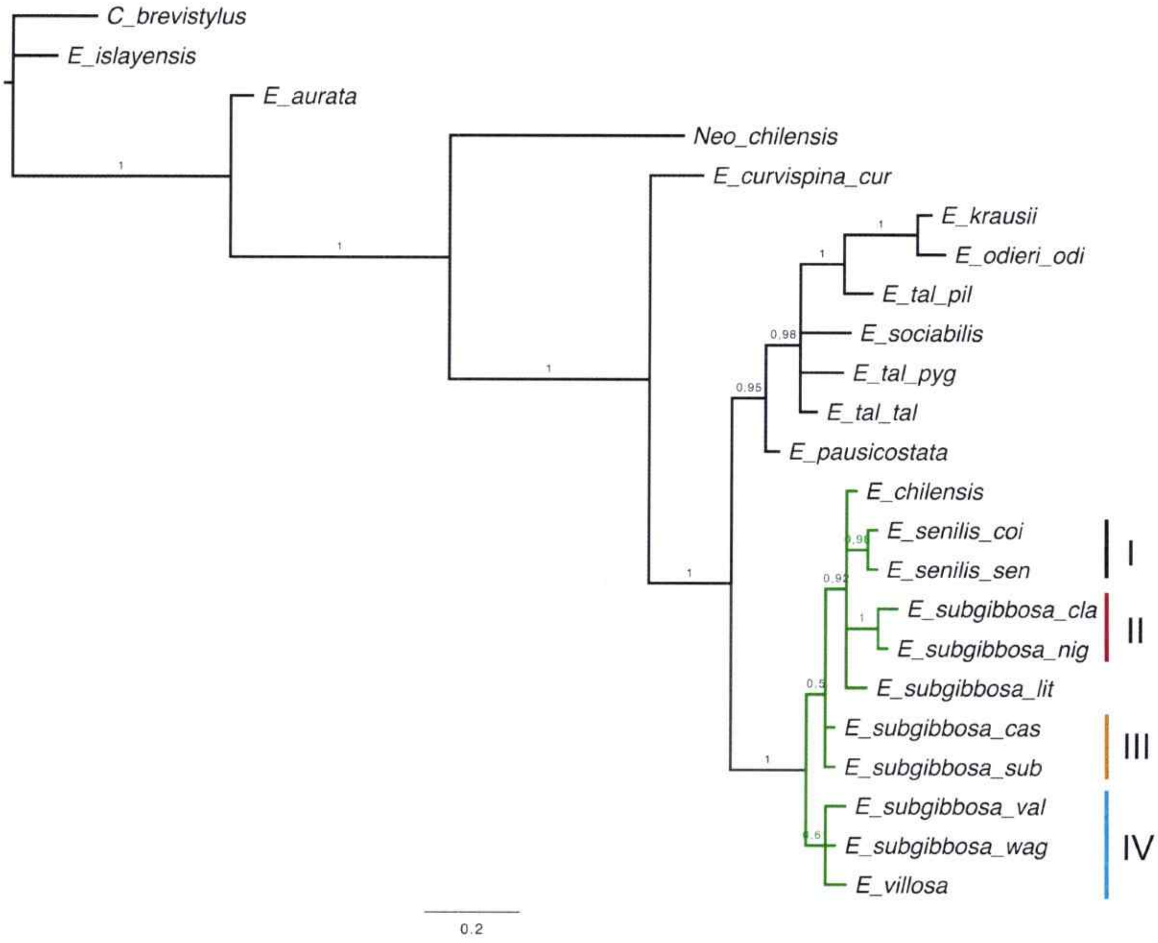

Figure IV.2. Bayesian phylogeny of *Eriosyce* subgen. *Neoporteria* (Cactaceae). Roman numbers indicate sister taxa analyzed in this study.

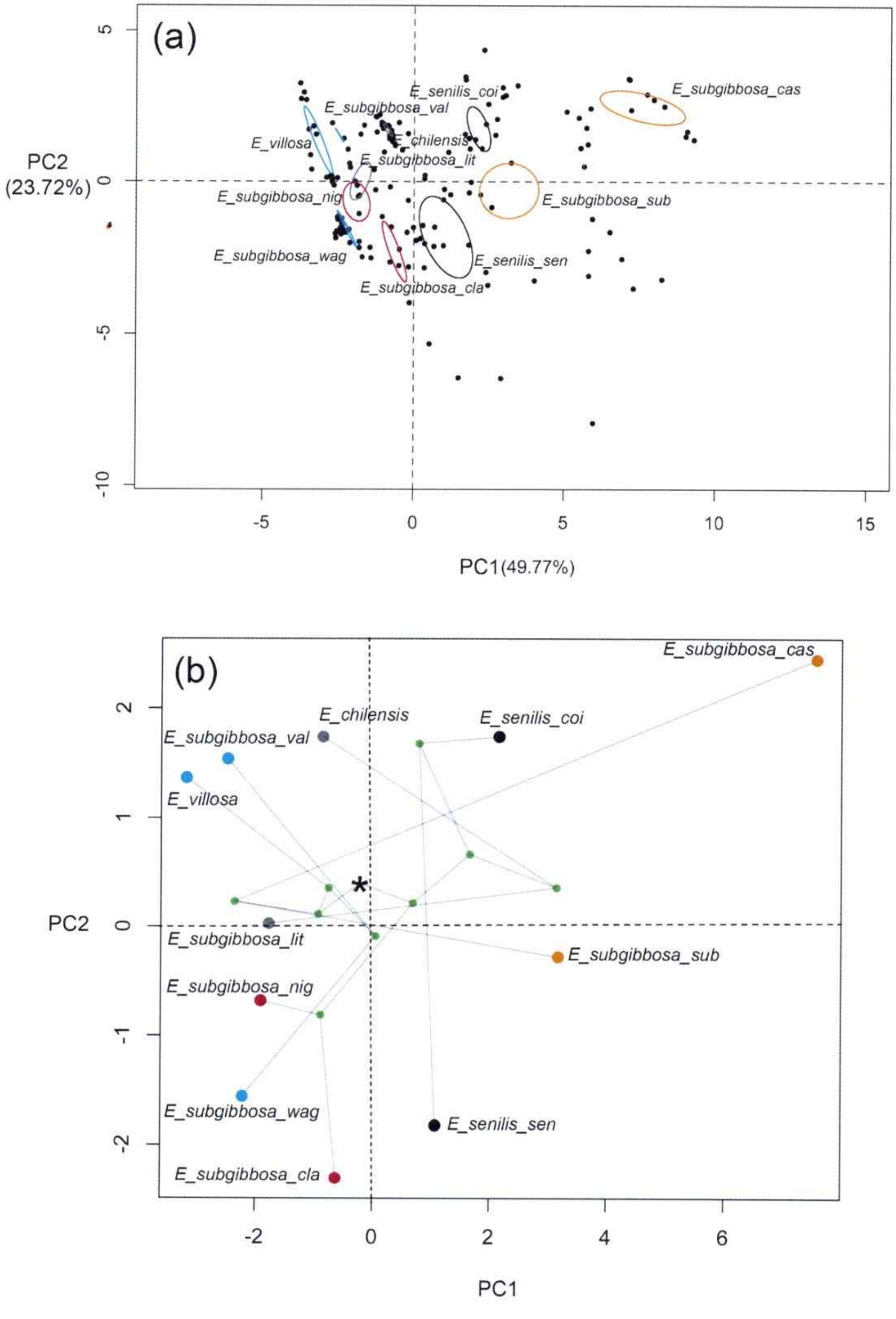

Figure IV.3. (a) Principal components analysis depicting the position of the 11 taxa of the *Eriosyce* subgen. *Neoporteria* (Cactaceae) clade in climatic–niche space, with each data point representing one–locality factor score of each given taxon, and ellipses represents the barycentre of taxa. (b) Phyloclimaticspace of the *E.* subgen. *Neoporteria* (Cactaceae) clade, with large circles representing the mean factor scores for a given taxon, and small green points represents ancestral nodes with their reconstructed factor scores. Identical colors of ellipses and terminal braches indicate sister taxa. Root is indicated with an asterisk. Note that PC1 is correlated with latitude and PC2 to elevation.

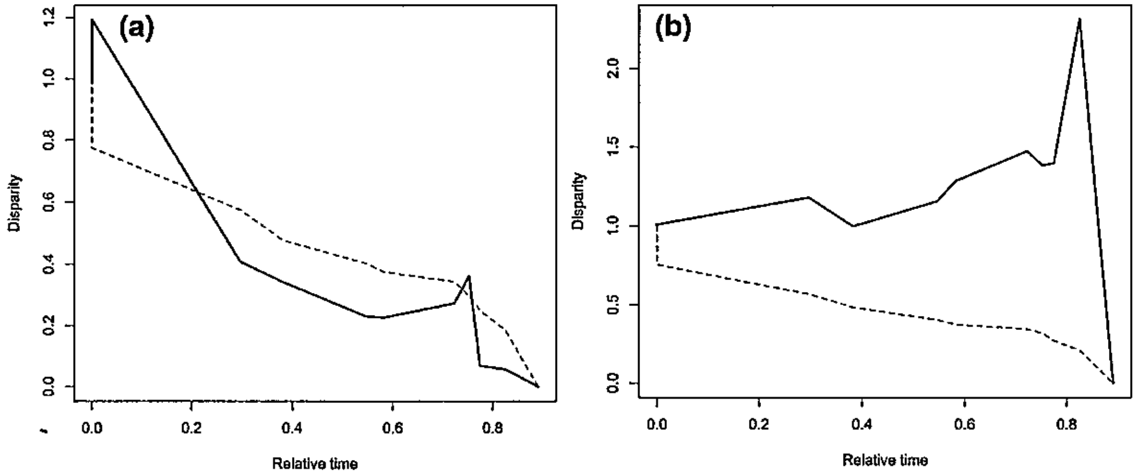

Figure IV.4. Relative disparity as a function of time for *Eriosyce* subgen. *Neoporteria* (Cactaceae) (solid line), compared with mean disparity from 1,000 simulations of Brownian motion evolution of that trait (dashed line). a, First principal component (PC1); b, second principal component (PC2).

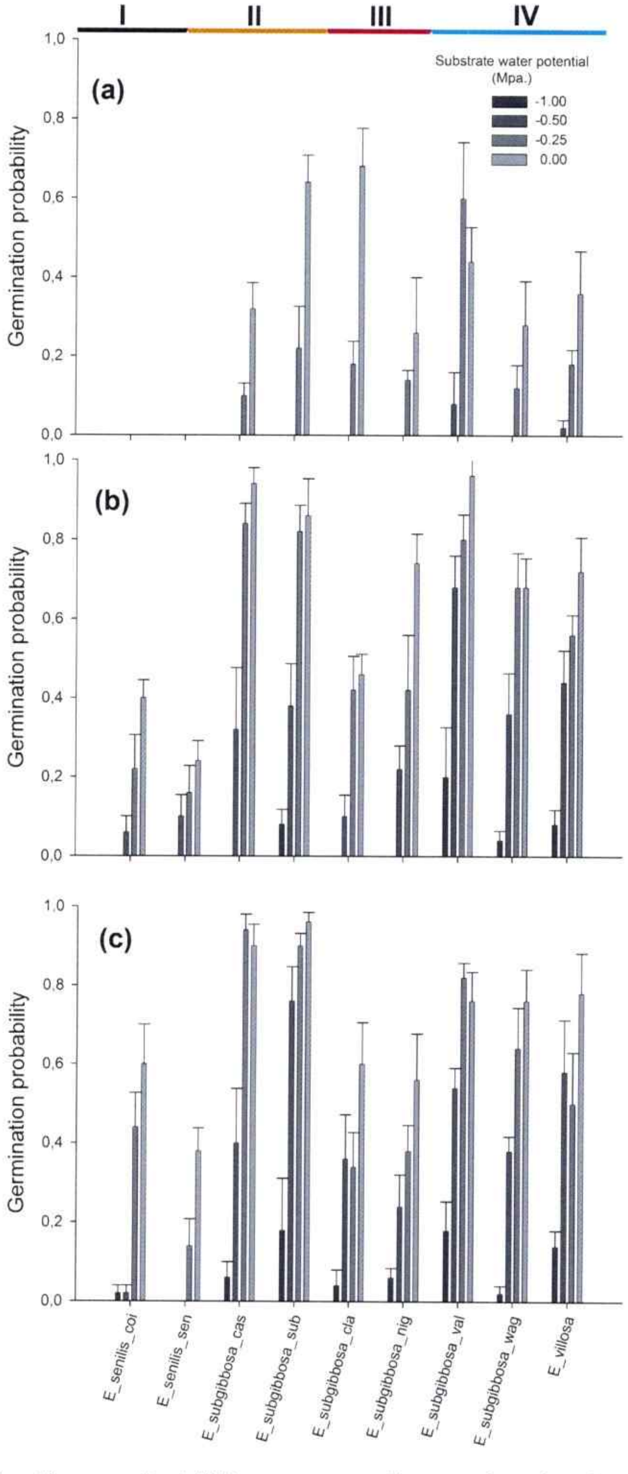

Figure IV.5. Germination probabilities among the endemic clade *Eriosyce* subgen. *Neoporteria* (Cactaceae) at three different night–day temperatures and substrate water potential conditions. a, night–day temperatures of 4–9°C; b, night–day temperatures of 11–15°C; night–day temperatures of 16–21°C. Colors and roman numbers indicate sister taxa. Bars show means ± S.E.

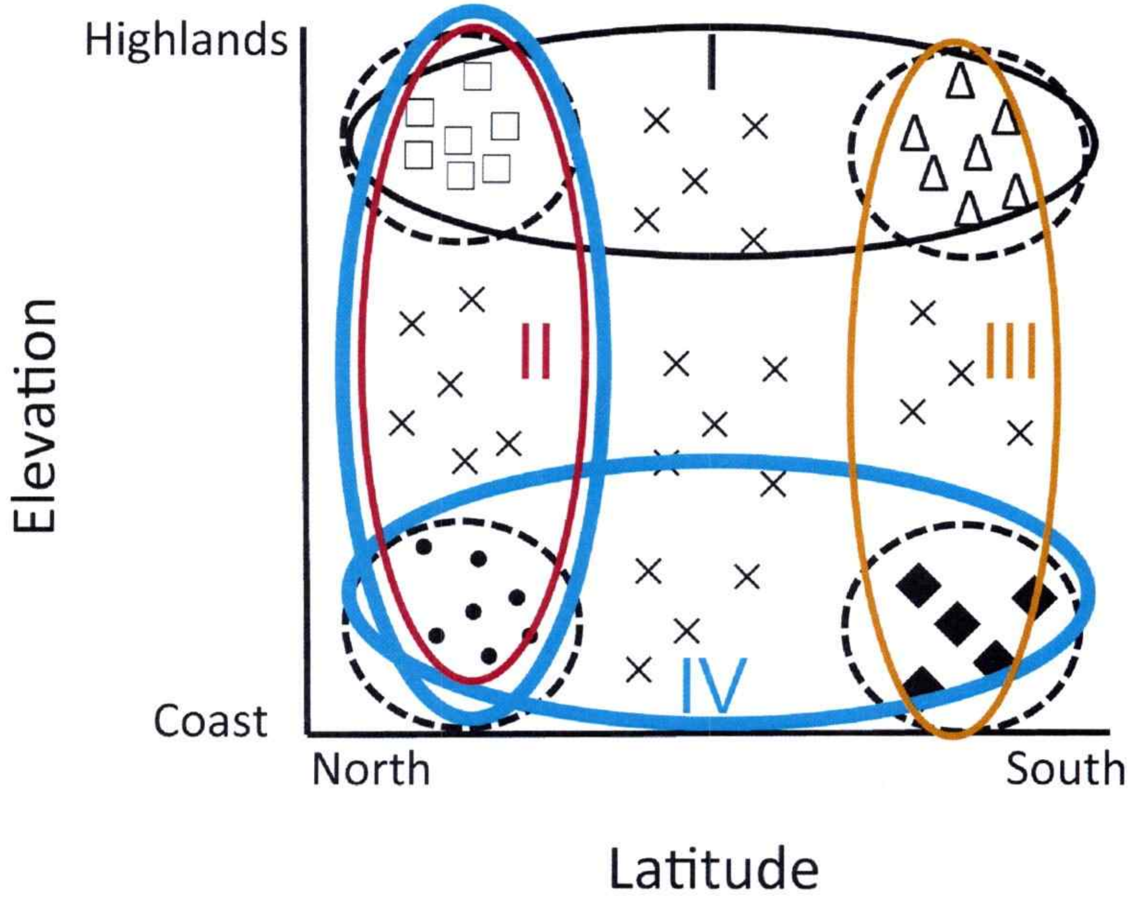

Figure IV.6. Hypothetical example illustrating how wet–dry phases might produce vicariant allopatric divergence along latitudinal and elevational gradients in central Chile. Squares, points, rhomboids and triangles represent occurrence localities of four taxa within a clade. Black circles and crosses correspond to current the geographic range of taxa and absences, respectively. Continuous circles represent the hypothetical distribution of the ancestral species that covered intermediate localities during a wet phase (with more gently climatic gradients). After an aridization process the ancestral geographic range split into two or more new taxa because intermediate areas are climatically unsuitable.

CAPÍTULO V: DISCUSIÓN GENERAL

En esta tesis se analizaron los efectos de los gradientes geográficos (i.e. altitud y elevación) y climáticos (i.e. temperatura y precipitaciones) sobre los patrones biogeográficos de las Cactáceas endémicas al Desierto de Atacama y Chile mediterráneo. Adicionalmente, para determinar el mecanismo que relaciona los gradientes climáticos con la diversificación se analizó en detalle el proceso de divergencia del grupo *Eriosyce* subgen. *Neoporteria* (= *Neoporteria*) en relación al nicho climático y germinativo. Los resultados obtenidos en este trabajo reflejan una estrecha relación del clima con la biogeografía y evolución de cactáceas, en que gradientes, barreras y cambios climáticos históricos darían forma a ciertos patrones: (i) concentración de la riqueza de cactáceas en latitudes medias y bajas altitudes, (ii) divergencia de *Neoporteria* inducido por la evolución del nicho climático.

V.1 CONCENTRACIÓN DE LA RIQUEZA DE CACTÁCEAS EN LATITUDES MEDIAS Y BAJAS ALTITUDES

Los patrones de riqueza y rangos de distribución de las 72 especies de cactáceas endémicas del Desierto de Atacama varían con la latitud y la elevación. Sin embargo el patrón endemismos no varia de igual manera en ambos gradientes, en un sentido latitudinal el patrón de variación, con un efecto del dominio medio, sugiere que los bioclimas tropical hiperdesértico (< 28°S, "norte grande" de Chile) y templado (> 37°S, sur de Chile) constituyen barreras "duras" (*sensu* Colwell y Hurtt 1994) para cactáceas y otras angiospermas (Arroyo *et al.* 1998; Kraus 1995; Luebert y Pliscoff 2006). Además, la dinámica climática de ambos sectores podría estar relacionada con la separación de dos grandes áreas de endemismos, una zona norte (18°-26°S) posiblemente modulada por la variación climática del Desierto de Atacama (bioclima tropical hiperdesértico) y una zona sur (27°-36°S) posiblemente modulada por la variación climática del centro-sur de Chile (bioclima templado) (Samaniego y Marquet 2009),. Cambios climáticos han ocurrido en diferentes momentos históricos (Lamy *et al.* 2001; Maldonado *et al.* 2005; Wara *et al.* 2005; Maldonado y Villagrán 2006; Nester *et al.* 2007), generando en algunos casos una intensificación de la aridez provocando cambios en la distribución de plantas y favoreciendo diversificación de diferentes linajes de plantas (Dillon *et al.* 2009; Placzek *et al.* 2009; Luebert *et al.* 2011). Por ejemplo una fase fría, el clima habría sido más húmedo en el Desierto de Atacama favoreciendo la colonización de la zona norte, mientras que las restricciones existentes en la zona sur se habría intensificado debido a la baja de temperaturas y alta humedad en Chile central (Arroyo *et al.* 1988; Villagrán 1994; Latorre *et al.* 2005; Placzek *et al.* 2009). Por el contrario, durante una fase cálida el Desierto de Atacama intensificaría su aridez generando extinciones en el extremo norte y segregaciones poblacionales en la periferia del desierto y centro de Chile, mientras que el clima del centro sur de Chile tendería a ser más cálido y menos lluvioso (Arroyo *et al.* 1988; Villagrán 1994; Lamy *et al.* 2001; Latorre *et al.* 2005; Placzek *et al.* 2009).

En el eje altitudinal, la variación de la riqueza de especies se concentra a bajas altitudes disminuyendo con la elevación. Adicionalmente, la configuración climática que co-varía con la elevación no sería una barrera "dura" sino que una restricción gradual para la sobrevivencia de cactáceas (Stevens 1992), ya que algunas especies han evolucionado tolerancias climáticas que les permitan vivir en esas condiciones extremas (McCain 2010). La riqueza altitudinal de especies también debiera estar influenciada por los ciclos climáticos, principalmente debido a la expansión de los glaciares desde la cordillera hacia menores altitudes durante un periodo glacial podría generar extinciones a elevaciones mayores. Tal como ocurre en el caso de *Neoporteria* la mayor diversidad de Cactáceas se encuentra a latitudes intermedias y a bajas altitudes, sugiriendo fuertemente que el proceso de diversificación podría ser mayor respecto de los extremos (tal como en *Neoporteria*).

Las variables climáticas que explicaron con un mayor peso la variación en de la riqueza de cactáceas fueron la temperatura mínima del mes más frio, temperatura del cuarto más húmedo y la precipitación media anual. Las condiciones de frio extremo constituyen una restricción fisiológica relevante para las cactáceas de Chile y otras zonas geográficas (Kraus 1995; Mourelle y Ezcurra 1997b), debido a la baja capacidad de muchas cactáceas de tolerar el congelamiento (Anderson 2001). La relación entre riqueza de especies y temperatura estar asociada a la disminución del número de especies con la elevación (altas elevaciones poseen temperaturas extremas), este patrón altitudinal ha sido mostrado en el caso de animales ectodermos (McCain 2010). Adicionalmente, cuando las bajas de temperaturas ocurren en situaciones de alta humedad se desencadenan severas consecuencias fisiológicas que favorecen el ataque los patógenos (bacterias y hongos) (Zimmermann y Granata 2002). Comparativamente, este efecto climático sería menos intenso en el sentido altitudinal, debido a que con el aumento de la latitud aumenta el frio y las precipitaciones, mientras que con el aumento de la elevación aumenta el frio pero las precipitaciones decrecen con comparación con la costa: zonas altas son frías y secas, mientras que a mayores latitudes son frías y húmedas.

V.2 DIVERGENCIA DE *NEOPORTERIA* INDUCIDO POR LA EVOLUCIÓN DEL NICHO CLIMÁTICO.

La dinámica filogenética del nicho es una propiedad de un clado que puede estar relacionada con el proceso de divergencia geográfica a través de cambios climáticos históricos (Wiens 2004b; Wiens y Donoghue 2004; Pearman *et al.* 2008; Wiens *et al.* 2010). El grupo *Neoporteria* posee una dinámica del nicho climático tendiente a un aumento en la disparidad con el tiempo, evidenciando una ampliación en la tolerancia a distintas configuraciones climáticas durante el proceso de diversificación del clado. El patrón de aumento en la disparidad indica que el cambio de nicho en los subclados es hacia óptimos climáticos (modelo Ornstein–Uhlenbeck), lo que a su vez sugiere que podrían estar respondiendo adaptativamente a los gradientes climáticos de Chile mediterráneo (Butler y King 2004; Kozak y Wiens 2010a). Incipiente evidencia indica que el aumento en la disparidad de nicho climático podría estar asociada aumento en la tasa de especiación (Kozak y Wiens 2010b), en un escenario similar los gradientes climáticos en Chile mediterráneo podrían favorecer los procesos de especiación (aumentando la diversificación).

Análisis más detallados sobre la relación nicho-biotopo climático, junto con evaluaciones del nicho germinativo fundamental entre taxa hermas muestran cómo podría operar el mecanismo de divergencia en *Neoporteria*, aportando información relevante sobre cómo el mecanismo que favorece la diversificación podría ayudar a dar forma los patrones de riqueza en Cactáceas (Wiens y Donoghue 2004; Wiens 2011). En ese sentido la diferencia del nicho climático entre taxa hermanas podría impedir el flujo genético, debido a que el nicho y biotopo de cada taxón es diferente en el espacio climático y geográfico. Más aún, la disímil configuración climática existente en el espacio que se encuentra entre taxa hermanas (i.e. pseudo-ausencias) favorece la separación geográfica. Adicionalmente, dada la respuesta germinativa diferencial en relación a condiciones de temperatura y potencial osmótico del sustrato (experimentos de jardín común), se estableció que existen diferencias importantes en el nicho fundamental germinativo de las taxa de *Neoporteria*. Interesantemente, entre taxa hermanas existe un marcado conservatismo en la respuesta germinativa. El conservatismo del nicho germinativo fundamental podría ser un elemento crucial en la divergencia inicial entre taxa hermanas, debido a que luego de un cambio climático (i.e. intensificación del gradiente climático) el espacio geográfico intermedio podría ser inadecuado para la germinación, y por lo tanto, al estar fuera del nicho fundamental decrecer la tasa de regeneración, afectando negativamente la dinámica poblacional (Holt 2009) y favoreciendo la actual separación geográfica.

V.3 COMENTARIOS FINALES

Es ampliamente reconocido que los cambios climáticos inciden directamente sobre el patrón espacial de la biodiversidad (Hawkins *et al.* 2003; Wiens y Donoghue 2004). Sin duda, el mecanismo que relaciona los patrones de riqueza y los gradientes (climáticos) subyace en el proceso de diversificación, extinción y dispersión de los clados (Mittelbach *et al.* 2007; Wiens 2011). En particular, la dinámica filogenética de nicho podría ser un componente crucial en el entendimiento de esta relación a múltiples escalas taxonómicas y espaciales, debido a que el cambio o estasis de nicho en el tiempo estaría vinculada a procesos de diversificación de linajes completos a escala global (Hua y Wiens 2010; Buckley *et al.* 2010), como el proceso de divergencia a escalas espaciales y taxonómicas menores (Evans *et al.* 2009; Kozak y Wiens 2010b).

Si bien en el caso de *Neoporteria* el conservatismo filogenético de nicho climático puede ser menos relevante en mantener la separación geográfica entre especies hermanas, a una escala taxonómica mayor puede incidir sobre patrones macro-evolutivos de la familia. Por ejemplo, algunos linajes estarían evidenciando conservatismo filogenético de nicho al restringir completamente su distribución a hábitat similares, el género *Copiapoa* se encuentra casi exclusivamente a altitudes < 1.000 msnm (Schulz 2006). Producto de cambios climáticos podrían aumentar las tasas de extinción de las *Cactáceas* endémicas al intensificarse la aridez o el frio-humedad, debido a que habría una tendencia a la incapacidad de ampliar el nicho hacia esos extremos climáticos. Esa incapacidad indica un grado importante de conservatismo filogenético de nicho a nivel de familia. Ahondar hacia el conocimiento de la biogeografía histórica de la familia podría revelar más profundamente el mecanismo existente que relaciona diversificación, extinción y colonización geográfica (Wiens y Donoghue 2004). Sin embargo, la filogenia y tasas de diversificación de la familia aún es pobremente conocida, dificultando resolver el desafío que implica conocer con más precisión los mecanismos generales de diversificación de una de las familias de angiospermas más diversas de Chile.

La mayor parte de este estudio utiliza el "nicho de Grinnell" para realizar las inferencias macro-evolutivas de la relación nicho-biotopo (Soberón 2007; Colwell y Rangel 2009). Ese dominio de la dualidad nicho-biotopo se focaliza en los requerimientos de las especies, constituidos por el conjunto de condiciones ambientales que permiten sus sobrevivencias y reproducción. Si bien, existe consenso acerca de la relevancia de esa porción del nicho en la dinámica espacio temporal de los organismos (Pearman *et al.* 2008). El "nicho de Elton" (Soberón 2007) basado en el dominio del nicho que se focaliza en las interacciones biológicas podría tener consecuencias ecológicas y evolutivas en *Neoporteria.* Por ejemplo, efectos indirectos como la disminución de la riqueza y de visitas relativas de los polinizadores en zonas climáticas extremas pueden imponer restricciones selectivas al desempeño demográfico de plantas (Arroyo *et al.*, 1982; 1988). Además, la polinización podría tener un rol relevante en el posible origen híbrido de *E. chilensis* y en la evolución de los síndromes de polinización en el clado, puesto que existe una gran variación en la morfología floral y fenología entre las taxa (Guerrero *et al.* 2011c). Es por ello que futuros estudios que evalúen la importancia relativa del efecto del medio abiótico y biótico son necesarios para un entendimiento más completo sobre los procesos evolutivos en su conjunto.

Dentro de la complejidad inherente de incorporar el dominio biótico y abiótico del nicho dentro del marco conceptual que busca comprender la dinámica espacio-temporal de los organismos, surge como un desafío mayor la aplicación de ese conocimiento en predecir la respuesta de la diversidad ante el escenario de cambio global. La ampliación geográfica del desierto producto de la reducción en las precipitaciones en su periferia, junto con la destrucción de la capa vegetal, alteraciones en la dinámica de la neblina podrían provocar en un futuro la extinción de numerosas especies endémicas que actualmente se encuentran amenazadas. La ventana de oportunidad de usar el conocimiento de las especies aplicado a la conservación de la diversidad biológica está limitada a la velocidad y magnitud del cambio local y global, es por ello, que comprender las respuestas ecológicas y evolutivas de las especies en relación al clima pasado, actual y futuro debiera ser un foco de atención y de inspiración para científicos actuales y futuros.

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