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Chilean Bromeliaceae: diversity, distribution and evaluation of conservation status

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Abstract Chile is home to 23 species of Bromeliaceae, including 2 subspecies and 4 varieties. Twenty species are endemic to the country. We examined 883 herbarium specimens from 27 herbaria for our treatment of the Bromeliaceae for the "Flora de Chile". These data and field observations resulted in a comprehensive database that we used to generate distribution maps for each species. We applied ecological niche modelling to reveal distribution areas and centers of Bromeliaceae diversity. We further analysed the collecting dates of the herbarium specimens to assess possible changes in species abundance. In this study we assess the conservation status of the bromeliad species in Chile. IUCN categories were assigned to the 27 bromeliad taxa as follows: Critically endangered: 4, Endangered: 6, Vulnerable: 11, Near threatened: 2, Least concern: 4. No species has become "Extinct" up to now. We also put forth a hypothesis about their biogeographic history.

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Introduction

The family Bromeliaceae (Poales) comprises over 2,600 species in 56 genera (Smith and Till 1998). The family is restricted to the Neotropics with the exception of the single species *Pitcairnia feliciana* (A. Chev.) Harms & Mildbr. from western Africa. According to molecular studies (Givnish et al. 2004) the disjunct distribution is probably the result of a comparatively recent long range dispersal event. Bromeliads are well known for their morphological and ecological plasticity. Innovations like water-absorbing scales and tank habit as well as physiological adaptations like succulence and crassulacean acid metabolism (CAM) enabled the family to successfully invade xeric and epiphytic habitats and undergo considerable radiation there. This led to the family's dominance among neotropical epiphytes ($\sim$1,140 epiphytic species/46% of total species number), among which Bromeliaceae is outnumbered only by Orchidaceae ($\sim$20,000 epiphytic species; Gentry and Dodson 1987). Investigating the evolution and biogeography of Bromeliaceae therefore promises to provide insights into the evolution of epiphytes as well as of South American forest habitats, which are known for their high overall and epiphytic plant diversity (e.g., Mata Atlântica in Brazil). Early attempts to reveal the evolution of the recent bromeliads using morphological and anatomical character based phylogenies, or to infer the historical biogeography based on the existing knowledge of current species distributions were unsuccessful. This can be attributed to the extraordinary plasticity of the bromeliads. The situation changed, when methods were established to investigate genetic diversity and variability of DNA sequence data. The first comprehensive molecular phylogenies provided surprising results (e.g., Horres et al. 2000, 2007; Givnish et al. 2004, 2007; Schulte et al. 2005; Schulte and Zizka 2008). Although there is a steady increase in molecular data available to infer phylogenies, the resolution of the phylogenetic reconstructions is still insufficient in Bromeliaceae due to low genetic variability in the family. This could be the result of the family's comparatively young and rapid radiation, particularly for the subfamily Bromelioideae. Nevertheless, the molecular data at hand allow first (1) dating of bromeliad evolution (Givnish et al. 2004), (2) reconstruction of character evolution and evaluation of systematic value of morphological and anatomical characters, (3) reconstruction of historical biogeography.

The distribution of Bromeliaceae in the Neotropics extends from the southern USA to the south of central Chile and Argentina (*Fascicularia* in Chile, *Tillandsia* in Argentina). Centers of diversity of the family are the Mata Atlântica in Brazil, Andean slopes of Peru, Colombia, and Ecuador as well as Mexico and adjacent Central America. The family has its southwestern limit of distribution in Chile, where it is represented by 6 genera and 23 species, 2 subspecies and 4 varieties.

Chilean Bromeliaceae—high degree of endemism and biogeographical relevance

The 23 species, 2 subspecies and 4 varieties of Bromeliaceae occurring in Chile is comparatively low (Table 1). There are, however, several peculiarities making these representatives particularly interesting. First, is the high degree of endemism. Besides *Tillandsia usneoides*, *Tillandsia virescens*, and *Tillandsia marconae*, all species are endemic to Chile. Second, some of the endemic species, like *Tillandsia tragophoba* and *Deuterocohnia chrysantha*, have an isolated occurrence well separated from their close relatives or even the rest of the genus (Dillon 1991; Zizka 2003). In isolated areas they could be interpreted as relics, which were separated from the remaining distribution

Table 1 Bromeliaceae of Chile

Deuterocohnia	*(Puya)*
Deuterocohnia chrysantha (Phil.) Mez	*Puya berteroniana* Mez
Fascicularia	*Puya boliviensis* Baker
Fascicularia bicolor (Ruiz & Pav.) Mez	*Puya chilensis* Molina
Fascicularia bicolor subsp. *bicolor*	*Puya coerulea* Lindl.
Fascicularia bicolor subsp. *canaliculata* E.C. Nelson & Zizka	*Puya coerulea* var. *coerulea*
Greigia	*Puya coerulea* var. *intermedia* (L.B. Sm. & Looser) L.B. Sm. & Looser
Greigia berteroi Skottsb.	*Puya coerulea* var. *monteroana* (L.B. Sm. & Looser) L.B. Sm. & Looser
Greigia landbeckii (Griseb.) Phil.	*Puya coerulea* var. *violacea* (Brongn.) L.B. Sm. & Looser
Greigia pearcei Mez	*Puya gilmartiniae* G.S. Varad. & A.R. Flores
Greigia sphacelata (Ruiz & Pav.) Regel	*Puya venusta* (Baker) Phil.
Ochagavia	*Tillandsia*
Ochagavia andina (Phil.) Zizka, Trumpler & Zoellner	*Tillandsia geissei* Phil.
Ochagavia carnea (Beer) L.B. Sm. & Looser	*Tillandsia landbeckii* Phil.
Ochagavia elegans Phil.	*Tillandsia marconae* W. Till & Vitek
Ochagavia litoralis (Phil.) Zizka, Trumpler & Zoellner	*Tillandsia tragophoba* M.O. Dillon
Puya	*Tillandsia usneoides* (L.) L.
Puya alpestris (Poepp.) Gay	*Tillandsia virescens* Ruiz & Pav.

The recognized taxa are listed based on recent revisions and our own unpublished results

following climate changes caused by the uplift of the Andes from their near geographic neighbours east of the Andean cordillera (a long distance dispersal appears more unlikely in these cases). A third important issue is the comparatively isolated and basal systematic position of some of the Chilean endemic bromeliads, e.g., *Fascicularia*, *Ochagavia* and *Greigia*, within the subfamily Bromelioideae.

These recently discovered facts (Schulte et al. 2005; Schulte and Zizka 2008) are consistent with the results of Varadarajan (1990) on endemism in the genus *Puya*. He recognized that the Chilean Puyas form the southernmost of eleven centers of endemism in the genus.

Our biogeographic analysis based on the phylogenetic reconstructions led to the hypothesis that the genera *Ochagavia*, *Fascicularia*, and *Greigia* separated comparatively early from the majority of the species of subfamily Bromelioideae (Core Bromelioideae). Chilean bromeliad species are thus of special scientific interest regarding the evolution and biogeography of the group. Based on the molecular phylogenies, we put forth the hypothesis, that the semiarid, Mediterranean type habitats in central Chile where colonized by ancestral bromeliads stemming from more mesic, Andean habitats.

Our revision of the Bromeliaceae for the "Flora de Chile" led to the investigation of the present day distribution based on collection data and field observations, and we inferred the potential distribution area based on ecological niche modelling. Based on the results of this survey we explicitly want to test, whether:

1. the actual or potential distribution areas of Chilean Bromeliaceae correspond with areas of principal vegetation types;
2. a comparison of actual and potential distribution areas allows conclusions about the conservation status of the species;
3. we can infer the historical biogeography of Chilean Bromeliaceae based on distribution areas.

Materials and methods

Data source

In the course of the taxonomic treatment of the Bromeliaceae for the "Flora de Chile", herbarium collections from the herbaria B, BM, BR, CONC, F, FR, FRP, G, GH, GOET, HAL, HBG, K, KIEL, L, LG, M, MO, NY, P, RBG, S, SGO, US, W, WRSL, WU were revised and all collecting data digitized (Zizka et al. 1999, 2002, unpublished data). In total, distribution records from 883 specimens were included in the survey.

The time of collections was divided into four intervals: (1) 1920 and earlier, (2) 1921–1965, (3) 1966–1985, and (4) after 1985. We consider the frequency with which a species is recorded in collections as a proxy for species abundance in each time interval. We consider species that were collected often in recent years to be common, and species, that were only collected infrequently or not at all, as rare and potentially endangered. Of course this only provides a rough estimate, but combined with field observations represents the best available information on the conservation status of Chilean bromeliads.

Ecological niche modelling

We modelled species distributions using the program Maxent (Phillips et al. 2004) with collection data from 27 herbaria worldwide. The environmental data layers consisted of the

BIOCLIM climate datasets of Worldclim (Hijmans et al. 2005) and the SRTM digital elevation data. Since we had many historical specimens without GPS coordinates, we georeferenced these with the help of online Gazetteers (Geonet Names Server, Getty Thesaurus of Geographic Names) and Google Earth. We used the whole set of bioclimatic layers provided by Worldclim which includes measures of temperature and precipitation for the whole year with averages, maxima and minima, but also seasonal measures, e.g., values for the warmest, coolest, wettest and driest quarters of the year.

For the following species, no distribution models are provided: *Ochagavia elegans* and *Greigia berteroi* are restricted to the small Robinson Crusoe Island, which is not covered by the BIOCLIM data sets. Their conservation status was recently discussed by Ricci (2006). *Tillandsia tragophoba* and *T. marconae* are known from only one locality in Chile, therefore we could not generate an ecological niche modelling for these species.

We counted all predictions with a value >0.5 for a specific grid cell to generate a map of species richness. This was done using a VBA routine in Microsoft Access.

Taxonomic concept

L. B. Smith and G. Looser dealt with Chilean bromeliads previously (e.g., Smith and Looser 1934, 1935; Looser 1948; Smith and Downs 1974, 1977, 1979). However, these date back to the late 1970s, and there is a need for current revisions, which take into account living material, molecular data and updated distribution data. Rauh (1985b), Zöllner and Oyanedel (1991), Zizka (1992), and Wilkin (1996) described habitat and morphology of characteristic Chilean species, and Marticorena and Quezada (1985) list 24 species of Bromeliaceae in their important and comprehensive "Catálogo de la flora vascular de Chile". Since its publication, several taxonomic and nomenclatural changes have taken place. A detailed study of the distribution of the species has not yet been undertaken.

One of the authors (G.Z.) is preparing a taxonomic revision of the family for the "Flora de Chile": treatments for the genera *Deuterocohnia*, *Fascicularia*, *Greigia*, and *Ochagavia* and have already been published (Nelson and Zizka 1997; Will and Zizka 1999; Zizka et al. 1999, 2002; Zizka 2003; Zizka and Novoa 2004). The genus *Puya* has received considerable attention until very recently (Gourlay 1952; Varadarajan 1990; Varadarajan and Flores 1990; Ravenna 2000; Muñoz-Schick 2003; Hornung-Leoni and Sosa 2005, 2008). The treatment of the Chilean Puyas will be published soon. For the genus *Tillandsia*, the revision of *Tillandsia* subgen. *Diaphoranthema* (Till 1984, 1989) and the recent discovery of an enigmatic species, *T. tragophoba* (Dillon 1991), have provided important information. *T. marconae* was first recorded for Chile by Zizka and Muñoz-Schick (1993) and Till (1993).

Based on our taxonomic research and recent papers, some taxonomic questions were dealt with in the following way:

1. The small *Tillandsia* species from central and northern Chile is identified as *T. virescens* Ruiz & Pav., following the concept of Till (1984).
2. "Typical" representatives of *Puya alpestris* and *Puya berteroniana* are easily recognized, but a number of intermediates exist. For the moment, we keep the two as separate species.
3. *Puya quillotana* was described by Weber (1984) as a separate species. According to our investigation the variability of the species falls within *Puya chilensis*. We therefore consider it synonymous with the latter. Further investigation is necessary to finally

decide on this taxon and aberrant plants found in the area, from where this taxon was described.

4. Recently *Puya pumila* was described by Ravenna (2000). We regard the species synonymous with *P. alpestris*.
5. In *Puya coerulea*, usually four varieties are distinguished. Our field and molecular studies support close relationship of these groups. While typical members can be identified easily, lots of intermediates exist. Therefore the groups are kept as varieties.

Some confusion exists about the correct epitheton of *P. berteroniana*. Stuessy and Marticorena (1990) made an attempt to harmonize the various epithets of Chilean plant species honoring Carlos Bertero and changed the originally published name *P. berteroniana* to *P. berteroana*. According to the most recent ICBN (2006), this is not correct and *P. berteroniana* has to be kept as correct name (ICBN 2006, article 60.6, Ex. 14).

Puya gilmartinii, named in honour of Amy Jean Gilmartin, was changed to *Puya gilmartiniae*.

Conservation status

The classification of conservation status that we use follows the categories and criteria of the International Union for the Conservation of Nature and Natural Resources (IUCN; version 3.1; see URL: www.iucnredlist.org/info/categories_criteria2001). For the Chilean Bromeliaceae we had to apply the categories Critically Endangered (CE), Endangered (EN), Vulnerable (VU), Near Threatened (NT), and Least Concern (LC). An earlier evaluation of Chilean Bromeliaceae by Hoffmann and Flores (1989) provides important information for some taxa and is cited and discussed under the relevant species. Unfortunately, taxonomic and nomenclatural uncertainties hamper its use for many of the Chilean species.

Although we have the best available database to assess conservation status based on comprehensive collection data and field observations, a detailed survey of population status is lacking for almost all of the species. Extraordinarily well-studied is the situation of the flora of the Juan Fernández archipelago, which includes the bromeliad species *G. berteroi* and *O. elegans* (Ricci 2006).

Distribution and conservation status

Deuterocohnia

Deuterocohnia chrysantha is a very attractive bromeliad easily recognized by its perennial inflorescences (Zizka 2003), a typical character for the genus. Our molecular studies revealed the species as genetically distinct from other species of the genus, corresponding with its geographic isolation (R. Horres and G. Zizka, unpublished data). The ecological niche model (ENM) gives a potential distribution area which extends considerably beyond the documented distribution: the current distribution of the species is fairly restricted to coastal areas of Paposo in the 2nd region (Fig. 1a). There, the species occurs in high numbers. Hoffmann and Flores (1989) classified the attractive species as "Vulnerable". According to our field observations, the northernmost populations of this species (Antofagasta–Tocopilla) are now almost dead and many populations near Taltal appear to be in bad condition. Due to the restricted distribution area and these observations we regard the species as "Endangered".
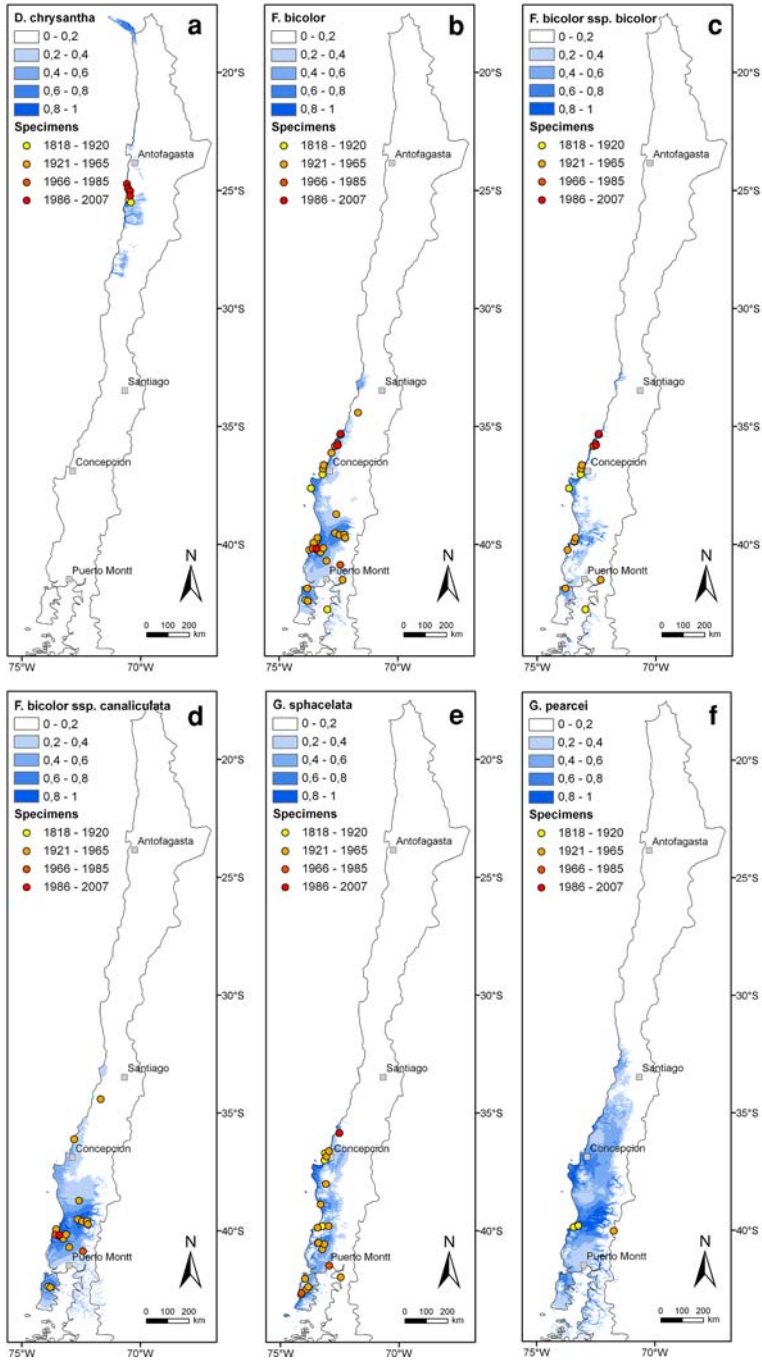
Fig. 1 Distribution of Chilean Bromeliaceae: *Deuterocohnia*, *Fascicularia*, and *Greigia*. The probability of presence as predicted by the Maxent models (0–1) is depicted. Specimen locations are indicated by *dots*, *coded* according to collection time. **a** *Deuterocohnia chrysantha*; **b** *Fascicularia bicolor*; **c** *Fascicularia bicolor* subsp. *bicolor*; **d** *Fascicularia bicolor* subsp. *canaliculata*; **e** *Greigia sphacelata*; **f** *Greigia pearcei*

Fascicularia

Distribution maps of the only representatives of this genus, *Fascicularia bicolor* subsp. *bicolor* and subsp. *canaliculata* were given and discussed in the recent revision (Nelson and Zizka 1997; Zizka et al. 1999). From the modelled distribution area (Fig. 1b) it becomes evident, that the species occurs in the area of the evergreen and laurifolious forest. The subspecies *bicolor* (Fig. 1c; IUCN category "Least Concern") is principally restricted to the coastal areas and grows usually in open habitats, while subsp. *canaliculata* (Fig. 1d; IUCN category: "Vulnerable") extends further inland and appears to be more shade-tolerant. In our opinion both taxa are comparatively common and have a considerable distribution area. We do not regard them as endangered but recommend monitoring their abundance, especially for subsp. *canaliculata*.

Hoffmann and Flores (1989) listed *F. bicolor* as "Vulnerable", and four additional species as "Insufficiently known". Due to nomenclatural confusions at that time, their classification cannot be assigned to valid names.

Greigia

The *Greigia* species from continental Chile are clearly restricted to humid and ±temperate climate. According to the vegetation map of Luebert and Pliscoff (2006) and the modelled distribution, they typically occur in the area of forest vegetation in temperate-humid climate as shadow-tolerant terrestrials in the understorey of evergreen, laurifolious and deciduous forests. Hoffmann and Flores (1989) classified *Greigia sphacelata*, *G. landbeckii*, *G. berteroi* as "Vulnerable", and *G. pearcei* as "Insufficiently known". Taxonomic uncertainties and nomenclatural confusions in *Greigia* hampered interpretation of their assessment. *G. sphacelata* (Fig. 1e) is the only species that was observed regularly and also collected recently (status "Vulnerable"). *G. pearcei* and *G. landbeckii* have not been collected and/or observed recently (Figs. 1f, 2a). We consider them "Critically Endangered" (*G. pearcei*) resp. "Endangered" (*G. landbeckii*). Especially *G. pearcei* seems to have been collected very rarely and may well be in danger of extinction. The niche modelling gives high probability for occurrence of *G. pearcei* and *G. landbeckii* almost as far north as Santiago. No field observations or collections support this, the northernmost records for these species being from the region of Concepción.

The endemic species from Robinson Crusoe Island, *G. berteroi*, was considered to be extinct. Ricci (2006, p. 3120) recently reported a remnant population of "… only six plants and no evidence of flowering and fruiting in Cerro Agudo, sector of Puerto Inglés" and classifies the species as "Critically Endangered".

Ochagavia

The genus *Ochagavia* has received some scientific attention, particularly due to the use of *Ochagavia litoralis* as an ornamental (Rauh 1985b; Zöllner and Oyanedel 1991; Zizka 1992; Zizka and Novoa 2004). The distribution has been discussed in the revision of Zizka et al. (2002). The models presented in Fig. 2b–d reveal the different ecology and climatic preferences of the three species in continental Chile: *O. litoralis* (Fig. 2a) mainly occurs in coastal habitats in central Chile. P.N. observed two centers of distribution with many individuals, one ranging from Valparaíso to San Antonio, and the other from Tanumé (north of Pichilemu) to Topocalma (south of Navidad). A few collections from further inland do exist, but they all predate the 1960s. P.N. observed small populations 15 km inland on rocky cliffs with
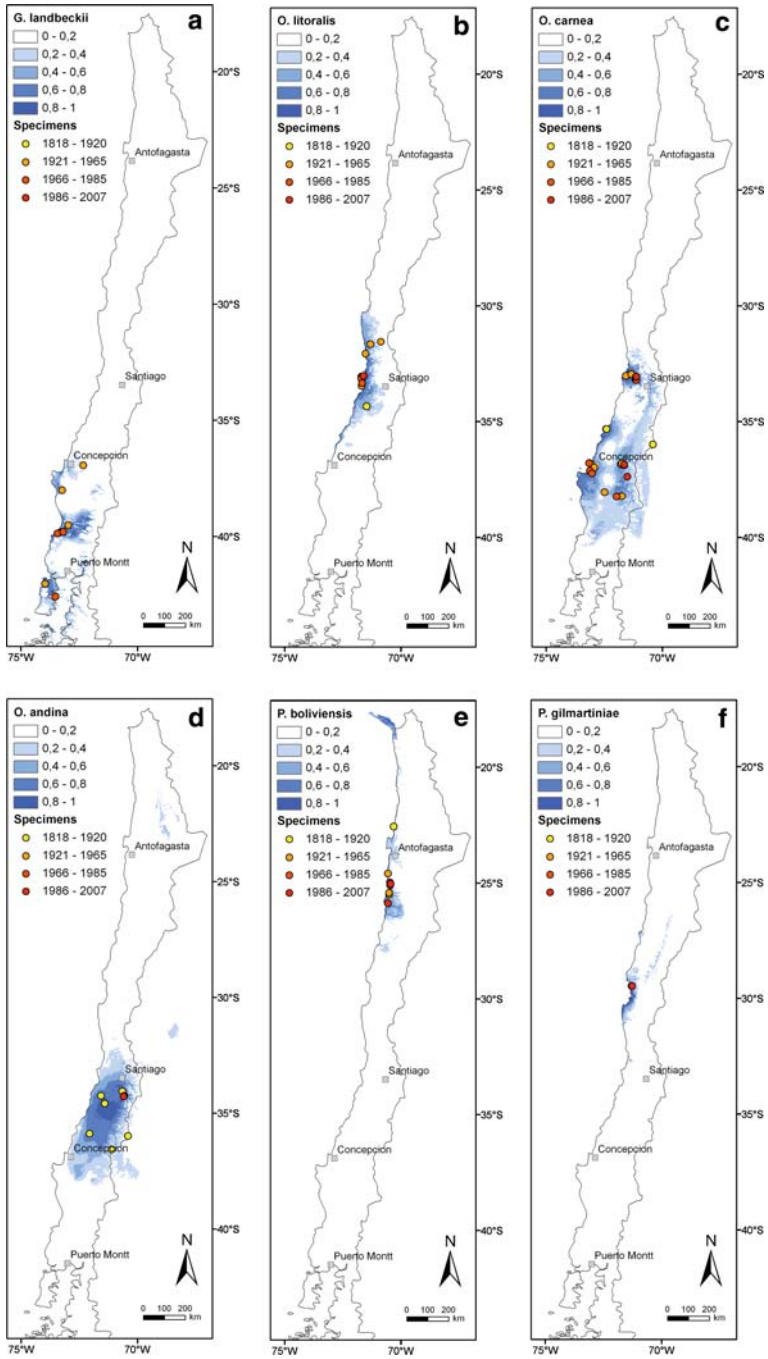
Fig. 2 Distribution of Chilean Bromeliaceae: *Greigia*, *Ochagavia*, and *Puya*. The probability of presence as predicted by the Maxent models (0–1) is depicted. Specimen locations are indicated by *dots*, *coded* according to collection time. **a** *Greigia landbeckii*; **b** *Ochagavia litoralis*; **c** *Ochagavia litoralis*; **d** *Ochagavia andina*; **e** *Puya boliviensis*; **f** *Puya gilmartiniae*

southern exposure near San Antonio and in "Salto del Agua", near Placilla. We regard these inland populations as rare and endangered thus principally restricting the species to a comparatively small strip along the coast of central Chile. Due to the extensive development and construction activities in this area, we classify the species as "Vulnerable".

Ochagavia carnea (Fig. 2c) has a wide distribution spanning from habitats near the coast to the Andean slopes. The modelled area is similar to the distribution of the deciduous forest, where we observed the species growing in shady undergrowth. The species was only rarely collected in recent times. We thus regard it to be "Vulnerable".

The most surprising data can be provided for *Ochagavia andina* (Fig. 2d), which had not been collected since 1907 and was considered extinct by Zizka et al. (2002). Due to the excellent field experience of P.N., the species was found and collected again in 2006 near Termas de Cauquenes at 697 m a.s.l. Although the observed population comprised numerous individuals, we consider the species "Endangered" and recommend that a targeted survey of the area is conducted. Old collections (made before 1890, except one from 1907) and the modelled area suggest the species historically had a relatively wide distribution area. Currently, *O. andina* is obviously restricted to a very limited area on the western slopes of the Andes at the eastern border of its former distribution. Again, due to taxonomic problems, the classification of Hoffmann and Flores (1989) is of little help. They consider *O. carnea* "Out of Danger" and *O. elegans* as "Vulnerable".

The remaining species, *O. elegans*, is endemic to Robinson Crusoe Island, where it is abundant on coastal cliffs. Ricci (2006) reports it from 19 localities, estimates the number of plants at over 2000 and classifies it at "Low Risk". Due to its very limited distribution, we think a classification as "Vulnerable" is more reasonable. *O. elegans* is cultivated in Botanic Gardens, e.g., in the Jardín Botánico Nacional Viña del Mar, which displays an impressive and uniquely diverse collection of Juan Fernández plants in its open grounds. *O. elegans* and its habitat have been described by Wilkin (1996) and Zizka (1992). Unfortunately, the harsh winter of 2007 in the area of Viña del Mar (lowest recorded temperature of $-3.4°C$ and 24 days with a minimum temperature below $0°C$) caused considerable losses to the unique collection at the Jardín Botánico Nacional.

Puya

For the Chilean *Puya* species, an updated revision is to appear soon (G. Zizka et al., in preparation). The genus suffers from nomenclatural confusions. The Chilean species are endemic to the country and form one of eleven centers of endemism sensu Varadarajan (1990). Chilean Puyas comprise a number of species of very limited distribution (*Puya gilmartiniae*, *P. boliviensis*) and some with extensive areas (*P. chilensis*, *P. alpestris*, *P. berteroniana*). The latter display extensive morphological variability across their distribution range, making the delimitation of species difficult, especially in the case of *P. alpestris* and *P. berteroniana*. Recent field observations of one of the authors (P.N.) give additional evidence for further infraspecific groups within these taxa.

We are presently assessing the difficult infraspecific relationships in the widespread species *P. chilensis*, *P. alpestris*, and *P. berteroniana* using amplified fragment length polymorphisms (AFLPs). We expect to be able to solve remaining questions about species delimitation and infraspecific diversity. Apparently, hybridisation between these three species seems to occur, enhancing the problem of taxon delimitation. Nevertheless, the current knowledge offers a sound basis for analysing the distribution and conservation status at species level, and we did not focus on infraspecific groups within the three species.

Puya boliviensis is morphologically quite similar to *P. chilensis*, but smaller in all parts and the inflorescence bears less branches. *P. boliviensis* (Fig. 2e) is geographically fairly isolated from the remaining Puyas. We only observed the species in habitats close to the coast in Quebradas that regularly receive humidity from coastal fogs. The modelled distribution exceeds the documented one, and interestingly extends north to the Chilean-Peruvian border. Due to the very restricted recent distribution we consider the species as "Endangered".

Among the remaining Chilean Puyas, *P. gilmartiniae* (Fig. 2f) stands out as an only recently described species (Varadarajan and Flores 1990) with an extraordinarily restricted distribution. To our knowledge, the single locality of the species is a foggy hilltop at 519 m a.s.l., not far away from the coast near the village of Chungungo, 4th region (Fig. 3). The modelled distribution area makes an occurrence in adjacent coastal areas in similar habitats likely and a survey of similar altitudinal ranges of coastal hilltops in this very sparsely inhabited area offers good chances to detect further populations of this species. It is morphologically well separated from other *Puya* species and easily recognized by its size and dense, white indumentum on the abaxial leaf surface and especially around the spines

Fig. 3 *Puya gilmartiniae* in its natural habitat

of the leaf margin. Due to its rareness, we regard the species to be "Critically Endangered". The Chilean Corporación Nacional Forestal (CONAF) has already taken measures to safeguard this rare species. Varadarajan and Flores (1990) described the population to comprise only 20 individuals. Protection of the only known locality and regular collecting of seeds and propagation in cultivation appears appropriate to us. It also is recommended to take the species into permanent cultivation, e.g., in the Jardín Botánico Nacional Viña del Mar, which might offer suitable climatic conditions.

Puya chilensis (Fig. 4a) is the most characteristic and easily recognized species of the genus in Chile. Its bright yellow flowers can be recognized from a distance, and the size of the glabrous leaf blades also allows easy identification in vegetative stage. *P. berteroniana* is of similar size (especially in inland habitats), and occurs sympatrically in part of the distribution area of *P. chilensis*. However, *P. berteroniana* has leaf blades with a dense abaxial indumentum of whitish scales. The astonishing turquoise colour of the flowers of *P. berteroniana* and the difference in flowering time are of course the easiest characters to differentiate the two species. Figure 4 a shows, that *P. chilensis* is distributed along the Coast, in the Coastal Cordillera, extends into the Central Valley, but does not inhabit the Andean slopes. It has been collected comparatively often and occurs in high abundance. A comparison with the vegetation map of Luebert and Pliscoff (2006) reveals that the distribution coincides quite well with the occurrence of Mediterranean type vegetation in central Chile (app. until 32°S, *P. chilensis* app. until 30°S). The modelled area is somewhat disjunct with two distribution centers, one around Concepción and one in the area of Santiago. We have no explanation for this and further field work in the area has to clarify, whether this hiatus really exists. As mentioned before, P.N. has recognized morphologically deviating populations in *P. chilensis* which point towards an infraspecific differentiation. These observations are now being assessed in using molecular data. The analysis of genetic similarity between the two distribution centers will be particularly interesting.

Puya berteroniana (Fig. 4b) and *P. alpestris* (Fig. 4c) are two other very characteristic and widespread species, which—unlike *P. chilensis*—have caused taxonomic and nomenclatural problems since their original description. These problems will be dealt with in the revision. As described above, two species are currently separated and display a quite clear geographic separation and clinal morphological variation throughout their extensive distribution. *P. berteroniana* is morphologically characterized by a size of 2–5 m and inflorescences with 50–100 branches, while *P. alpestris* is 1–2 (−2.5) m high and bears inflorescences with 15–20 (−30) branches. Typical representatives of both taxa are easily identified, but size tends to decrease towards south, so that especially in central Chile where the distribution areas of both groups come into contact intermediates are found that are difficult to assign to one of the groups. Both taxa have been extensively collected and are comparatively abundant throughout their area. A striking difference to *P. chilensis* is the extension of both species' ranges from the coast eastward to the Andes. The area of *P. alpestris* coincides well with the occurrence of the more humid seasonal Mediterranean bioclimate and sclerophyllous forest of southern central Chile (Luebert and Pliscoff 2006), while that of *P. berteroniana* corresponds to the more arid Mediterranean bioclimate types further north and the area of sclerophyllous shrub. Similar to *P. chilensis*, both species are characteristic for the Mediterranean type climate in central Chile and comparatively abundant in their habitats. They are considered as common (IUCN category "Least Concern"). Similar to *P. chilensis*, further infraspecific differentiation seems to occur in both groups and will be subject to future molecular studies.

Puya coerulea is a morphologically very variable group, whose distribution is also limited to the Mediterranean climates and sclerophyllous forest/Matorral vegetation (Figs. 4d–f, 5a,
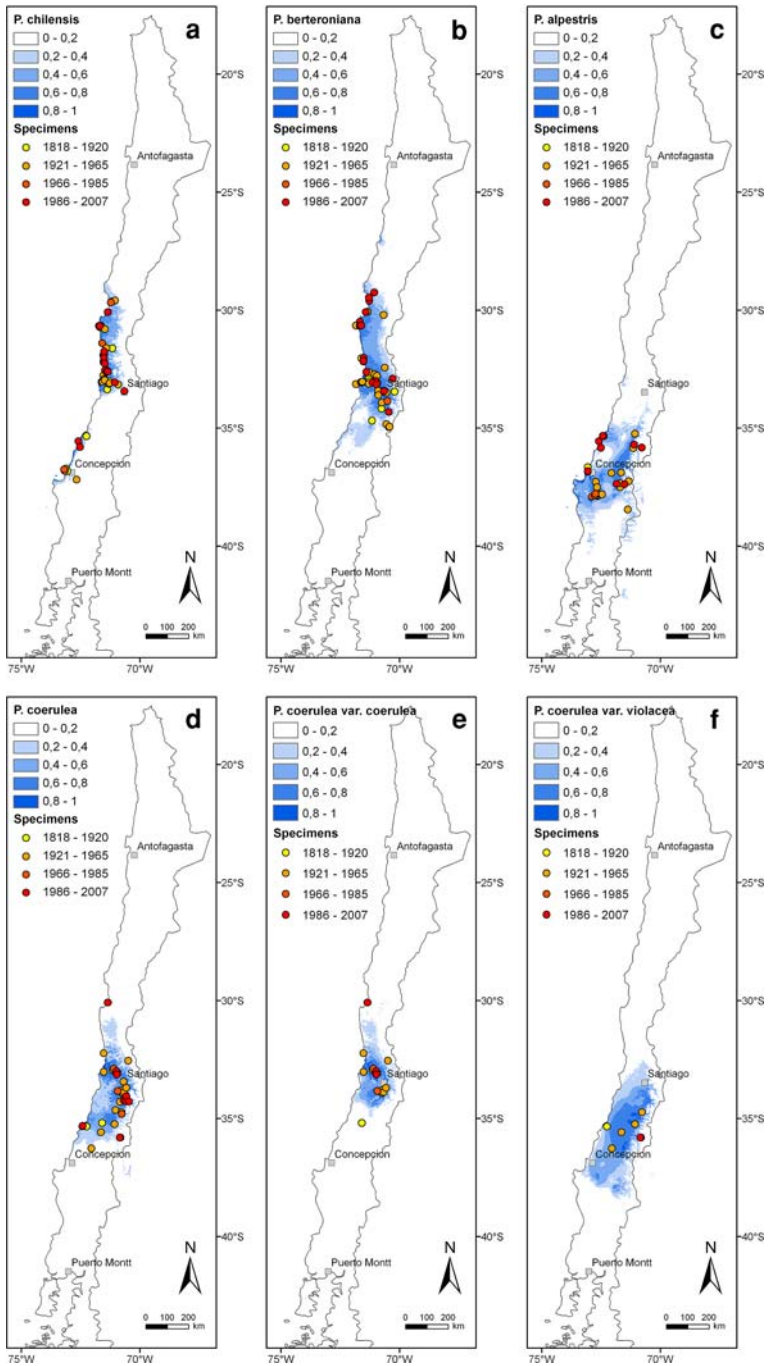
Fig. 4 Distribution of Chilean Bromeliaceae: *Puya*. The probability of presence as predicted by the Maxent models (0–1) is depicted. Specimen locations are indicated by *dots*, *coded* according to collection time. **a** *Puya chilensis*; **b** *Puya berteroniana*; **c** *Puya alpestris*; **d** *Puya coerulea*; **e** *Puya coerulea* var. *coerulea*; **f** *Puya coerulea* var. *violacea*

b). The astonishing diversity in inflorescence characters and proportions (pedicel vs. bract, distance of flowers) led to different taxonomic concepts. Our field observations confirm the widely accepted concept of Smith and Looser (1935) which recognises four varieties in the species *P. coerulea*. Typical representatives of the varieties are easily identified, but high variability and intermediates do occur. Additionally, morphologically different groups (flower colour) occur in this highly variable taxon, although they are currently not recognized taxonomically. *P. coerulea* var. *coerulea* appears to be the only group that is restricted to the Coastal Cordillera, while the others are found principally on the western slopes of the Andes. Var. *violacea* and var. *intermedia* as well as var. *monteroana* and var. *intermedia* occur sympatrically. From our observations the *P. coerulea* varieties *intermedia* and var. *coerulea* are most widespread and most abundant. We classify them as "Near Threatened". The remaining varieties were observed in few localities with populations of considerable size and are considered "Vulnerable" based on their limited distribution. Possibly, the historic distribution of the latter three taxa extended further west, but may have become restricted recently by human impact. We recommend protecting existing populations and monitoring their development. At least two varieties were abundant at the locality where *O. andina* occurs and could be protected together with that species.

Puya venusta (Fig. 5c) displays another distribution pattern within Mediterranean semi-arid climates in central Chile from Los Molles (32°14′S, 250 mm annual precipitation) to Tongoy (30°15′S, 80 mm) with a disjunct population in Zapallar forming the southern limit at 32°33′S. The species is principally restricted to coastal habitats and often occurs in high abundance, forming dense stands. It is easily recognized and taxonomically well defined. According to observations of P.N., there is evidence for hybridisation with *P. chilensis* near the northern distribution limit (Zapallar, 32°33′S, 71°28′W), where both species occur sympatrically. This appears to be the first record of hybridization between species of the two subgenera *Puya* and *Puyopsis*. The Universidad Católica de Valparaíso is at present investigating these populations (M. Cisternas, personal communication). *P. venusta* is considered "Vulnerable" due to the intensive development and construction activities in its habitats.

The important assessment of the conservation status of the Chilean Puyas by Hoffmann and Flores (1989) is now outdated and was probably based on rather few data (*P. alpestris* "Rare", *P. berteroniana* "Vulnerable"; *P. boliviensis* "Rare"; *P. chilensis* "Vulnerable"; *P. coerulea* var. *coerulea* "Out of Danger"; *P. coerulea* var. *intermedia* "Vulnerable"; *P. coerulea* var. *monteroana* "Insufficiently known"; *P. coerulea* var. *violacea* "Vulnerable"; *P. venusta* "Vulnerable").

Tillandsia

Dillon (1991) described the very rare endemic *T. tragophoba* and estimated the population size of 100–200 scattered individuals. The species is known only from a very restricted locality near Paposo, Antofagasta region. The systematic relationships of this bromeliad remain unclear, but its tank habit, typical for *Tillandsia* species growing in far more humid environments in forest vegetation of the Andes points toward a relationship as suggested by Dillon (1991). It supports also the hypothesis, that the present occurrence is a relict of a former wider distribution of the vegetation found in the region of the coastal fog belt ("camanchaca"). The species is now well known and a considerable number of botanical field trips have been undertaken to the fog-desert areas near Paposo. The species has not been recorded from any additional localities, and we consider it a very local endemic and "Critically Endangered". No modelling was done for the species, as it is known from only a single locality.
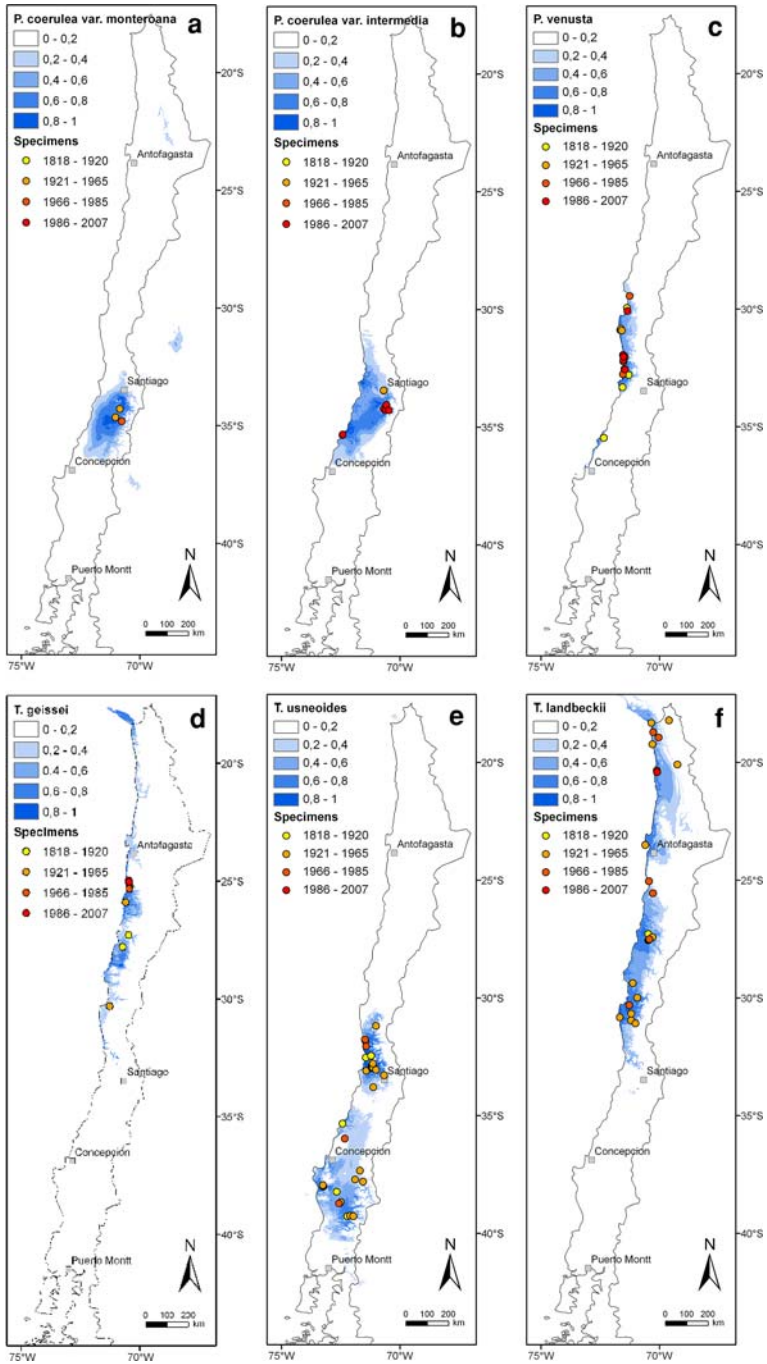
Fig. 5 Distribution of Chilean Bromeliaceae: *Puya* and *Tillandsia*. The probability of presence as predicted by the Maxent models (0–1) is depicted. Specimen locations are indicated by *dots*, *coded* according to collection time. **a** *Puya coerulea* var. *monteroana*; **b** *Puya coerulea* var. *intermedia*; **c** *Puya venusta*; **d** *Tillandsia geissei*; **e** *Tillandsia usneoides*; **f** *Tillandsia landbeckii*

Tillandsia geissei (Fig. 5d) is an epiphytic species that regularly occurs in the fog influenced vegetation of the western slopes of the Coastal Cordillera in the region of Paposo. Here it has been observed in the last decades. Older collections document a distribution further south and north. No recent confirmations are at hand, probably due to population decreases. A survey of this species of fog influenced habitats near the northern and southern border of the modelled distribution would help to answer this question and also give important information about the development of the "camanchaca" vegetation. Due to obviously very limited distribution range and narrow ecological niche we classify *T. geissei* as "Endangered".

Tillandsia usneoides (Fig. 5e), the well known and most widespread of all Bromeliaceae, has an unusual distribution in Chile. Is has been collected often from numerous localities, and the distribution model clearly documents its occurrence in central Chile. The distribution corresponds with the areas of the deciduous and sclerophyllous forests (Luebert and Pliscoff 2006). However, upon examining collecting periods, it appears that no recent collections are at hand, nor was the species observed by the authors during the field trips in the last years. Similar to *T. geissei*, *T. usneoides* is an epiphytic *Tillandsia* without roots in adult stage, relying totally on the highly specialized scales for water and nutrition uptake from atmospheric humidity. Therefore, *T. usneoides* and *T. geissei* can be regarded to be sensitive indicators for changes in atmospheric humidity and the investigation of their distribution dynamics might give important information about these environmental changes. Because of lack of recent collections we define the conservation status of *T. usneoides* as "Vulnerable".

Tillandsia landbeckii (Fig. 5f), another atmospheric *Tillandsia*, displays a fascinating ecology. It is one of the desert Tillandsias from the hyperarid regions of northern Chile and southern Peru that grow on the desert sand and require regular fog humidity to survive (Rauh 1985b; Rundel et al. 1997; Pinto 2005; Pinto et al. 2006). A similar strategy is also reported for *T. marconae*, *T. latifolia*, *T. purpurea*, *T. paleacea*, and *T. werdermannii*. Due to recent field studies and further studies of R.P., we have very detailed knowledge of the distribution of *T. landbeckii* in northern Chile. The species occurs in vast pure stands in various localities along the coastal Cordillera southward to the Loa river (21°S). Due to its extreme specialisation and dependence on fog humidity, we consider this species to be "Vulnerable".

Tillandsia marconae is poorly documented and was first described for Chile only recently (Zizka and Muñoz-Schick 1993). Very little information about its distribution is at hand. It is obviously a very rare species (Till and Vitek 1985; IUCN category "Endangered"). A hybridogen origin of the species has been discussed, *T. landbeckii* and *T. purpurea* being possible parental species. No modelling was performed for this taxon.

Tillandsia virescens (Fig. 6) belongs to the taxonomically difficult group of *Tillandsia capillaris* Ruiz and Pav. (Till 1984, 1989), comprising mostly small atmospheric Tillandsias that grow epiphytically or are saxicolous. The very similar species display high morphological plasticity and therefore were often misidentified. In our treatment we follow the species delimitation and nomenclature of Till (1984), according to which the specimens are identified as *T. virescens*, a species distributed also in Peru, Bolivia, and N-Argentina (IUCN category "Vulnerable"). Most of the records from Chile and the modelled distribution display occurrences in the drier Mediterranean climate of northern central Chile, corresponding with the Matorral vegetation (Pinto 2001). Two collections stem from the northernmost part of Chile, more than one thousand km away from the remaining distribution and collected at high Andean elevations, where R.P. has observed additional populations recently. Investigation of these populations with molecular methods appears appropriate to reveal their genetic relationships and biogeographical links.

Fig. 6 Distribution of Chilean Bromeliaceae: *Tillandsia virescens*. The probability of presence as predicted by the Maxent models (0–1) is depicted. Specimen locations are indicated by *dots*, *coded* according to collection time
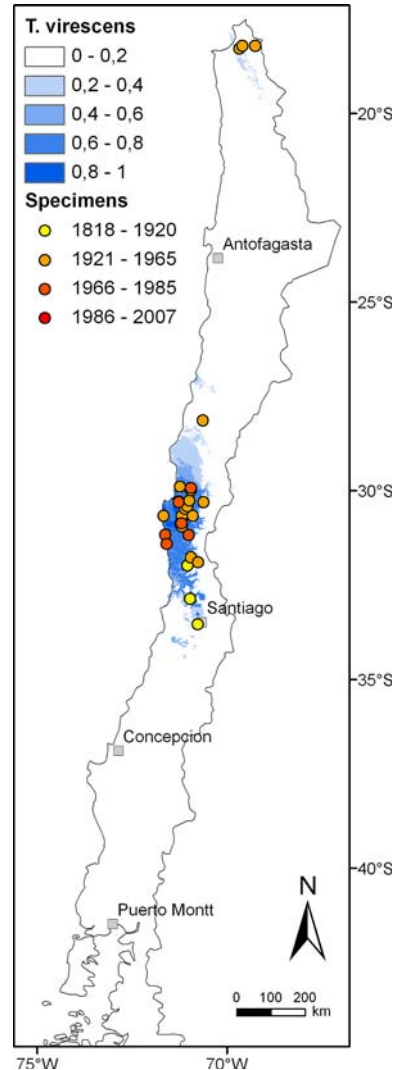
The earlier evaluation of Hoffmann and Flores (1989) lists *T. virescens* ("Vulnerable"), *T. geissei* ("Vulnerable"), *T. landbeckii* ("Vulnerable"), and *T. usneoides* ("Vulnerable"). *T. tragophoba* had already been collected in 1988 but was not yet described at that time (Table 2).

Discussion

Diversity pattern

Figure 7 sums up the distribution data and displays the Bromeliaceae diversity in continental Chile. Two centers of diversity are found in central Chile, separated by a low diversity area at about 35°S. Highest diversity is found in the coastal areas and adjacent

Table 2 Chilean bromeliad species and their conservation status

Species	Conservation status
Deuterocohnia chrysantha	Endangered
Fascicularia bicolor	
Fascicularia bicolor subsp. *bicolor*	Least concern
Fascicularia bicolor subsp. *canaliculata*	Vulnerable
Greigia berteroi	Critically endangered (Ricci 2006)
Greigia landbeckii	Endangered
Greigia pearcei	Critically endangered
Greigia sphacelata	Vulnerable
Ochagavia andina	Endangered
Ochagavia carnea	Vulnerable
Ochagavia elegans	Vulnerable
Ochagavia litoralis	Vulnerable
Puya alpestris	Least concern
Puya berteroniana	Least concern
Puya boliviensis	Endangered
Puya chilensis	Least concern
Puya coerulea	
Puya coerulea var. *coerulea*	Near threatened
Puya coerulea var. *intermedia*	Near threatened
Puya coerulea var. *monteroana*	Vulnerable
Puya coerulea var. *violacea*	Vulnerable
Puya gilmartiniae	Critically endangered
Puya venusta	Vulnerable
Tillandsia geissei	Endangered
Tillandsia landbeckii	Vulnerable
Tillandsia marconae	Endangered
Tillandsia tragophoba	Critically endangered
Tillandsia usneoides	Vulnerable
Tillandsia virescens	Vulnerable

parts of the coastal cordillera. The climate is of Mediterranean nature throughout and the natural vegetation in this region comprises deciduous and sclerophyllous forests in the south and different types of sclerophyllous shrub (matorral) in the north. Species with considerable distributions in both subareas are *P. chilensis*, *P. coerulea*, *P. venusta*, and *T. usneoides*. Further species are centered in the northern (*O. litoralis*, *P. berteroniana*, *P. gilmartiniae*, *T. virescens*) or southern subarea (*P. alpestris*, *F. bicolor* subsp. *bicolor*, *G. landbeckii*, *G. sphacelata*, *O. carnea*).

Some species of the southern subarea like *F. bicolor*, *O. carnea*, *G. sphacelata*, and *G. landbeckii* extend further south into the area of the temperate evergreen forests, where *G. pearcei* has its center of distribution. These "forest species" belong to the basal groups among Bromelioideae and probably reached their present distribution through temperate-humid Andean habitats (Schulte et al. 2005; Schulte and Zizka 2008). One species closely related to *O. carnea*, *O. andina*, is presently restricted to Andean habitats.

Fig. 7 Species richness of Chilean Bromeliaceae obtained by counting all species with a probability of presence of at least 0.5. The position of protected areas is taken from the world database on protected areas (WDPA, http://www.unep-wcmc.org/wdpa/)
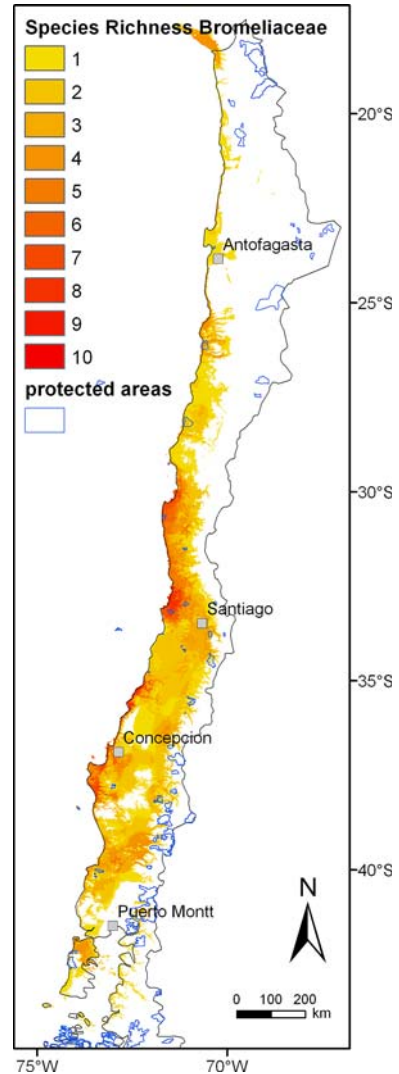
Puya boliviensis, *T. geissei*, *T. tragophoba*, *T. landbeckii*, *T. virescens*, *T. marconae*, and *D. chrysantha* are a heterogenous group centered in northern Chile, with *T. virescens* also being distributed in the northern subarea mentioned above. Most of them appear to be systematically and geographically isolated from their nearest relatives (if these are known at all), which at least in the case of *P. boliviensis*, *T. tragophoba*, and *D. chrysantha* do occur far away in the Andes or east of them. We consider their occurrences in northern Chile as relict habitats. This hypothesis is supported by other biogeographic relationships between species from the northern Chilean fog deserts and the humid Andean or trans-Andean habitats.

To explain different systematic position, ecological specialisation and extent of radiation among the Chilean bromeliads, we propose the following hypothesis about their biogeographic history: The species of the high diversity centers in central Chile and the

species extending further south to the temperate evergreen forest are mainly representatives of *Puya*, *Greigia*, *Ochagavia*, and *Fascicularia*. The first genus principally has an Andean distribution and is the sister group of subfamily Bromelioideae, which include the three other genera (Schulte et al. 2005). The other three genera form basal clades within the subfamily, which has its center of diversity in the Atlantic forests of eastern South America. *Puya* species generally occur in more or less temperate and humid conditions of the Andes, as do the species of *Greigia*. *Ochagavia* and *Fascicularia* are Chilean endemics and also restricted to temperate and humid habitats, at most extending to the southern subarea of the Mediterranean climate. Based on their molecular phylogenies Schulte et al. (2005) suggest that the predecessors of these genera where adapted to temperate and humid conditions and reached their present area via the Andes. We suggest, that the distribution of predecessors extended westward to the coast in climatically more humid geological times. *Ochagavia* and *Fascicularia* experienced a minor radiation in this region of the evergreen forests and in part also adapted to the Mediterranean type climate when conditions became warmer and dryer in central Chile (*O. litoralis*, *F. bicolor* subsp. *bicolor*). For the *Puya* species *P. chilensis*, *P. berteroniana*, *P. alpestris*, *P. coerulea*, and *P. gilmartiniae* we also postulate, that their predecessors spread from more mesic Andean habitats westward. A pattern of genera with predominantly Andean distribution like *Acaena* and *Rumex* occurring as far west as Laguna la Tagua Tagua in central Chile has been documented by Heusser (1990). When the climate in central Chile became drier and warmer, the *Puya* species adapted to more arid conditions and in part radiated there (species group *P. chilensis/Puya beteroniana/P. alpestris*, *P. coerulea*).

We have no hypothesis about the time frame of the process, but palynological studies of Heusser (1990) document a temperate and more humid climate for central Chile (area of Laguna la Tagua Tagua, 34°30′S, 71°10′W) about 50.000–35.000 years ago. Our systematic studies suggest, that the Chilean Puyas probably stem from two ancestors, each of which evolved into one species group, *P. chilensis/P. berteroniana/P. alpestris/P. gilmartiniae/P. boliviensis* and *P. coerulea/P. venusta*, respectively.

Most species centered in the north exhibit a different distribution. Apparently, *T. tragophoba* and *D. chrysantha* are systematically and geographically isolated. They are found in the peculiar coastal habitats in northern Chile, which regularly receive considerable humidity through coastal fogs, which support a local, but surprisingly diverse loma vegetation. No radiation is observed in these groups and we regard their habitats as relictual, postulating that in previously more humid times these areas were covered by more extensive vegetation, presumably with floristic links to tropical Andean habitats.

In spite of the extensive molecular studies of Barfuss et al. (2005) in subfamily Tillandsioideae, it is not yet possible to define closest relatives and thus hypothesize about area of origin and ecological preferences of predecessors of the atmospheric Tillandsias of northern Chile (*T. landbeckii*, *T. marconae*, *T. virescens*, *T. geissei*).

Taking their occurrence in extreme deserts in northern Chile and Peru into account, we can characterise them a group of ecological specialists that manage to grow in vast, often monospecific stands ("tillandsiales") on pure desert sand, which became secondarily rootless, relying entirely on regular fog humidity. Depending on the orographic situation and climatic conditions, fog corridors may enable growth of such tillandsiales more than 40 km away from the coast (Pinto et al. 2006; Rauh 1985a). *T. landbeckii*, *T. marconae*, and *T. virescens* represent this group in Chile, which includes also *Tillandsia latifolia*, *Tillandsia paleacea*, *Tillandsia purpurea*, *Tillandsia werdermannii* and *Tillandsia recurvata* from Peru. These highly specialised *Tillandsia* species might well be a product of adaptation of few predecessors to increasingly arid environment and subsequent

radiation. Nevertheless, without molecular phylogenies including those species, it appears premature to speculate about their systematic affinities and evolution. Recent studies of Barfuss et al. (2005) include only *T. marconae* from this group. A similar information deficit hampers the analysis of biogeographic relationships of *T. geissei*.

For the extremely widespread and easily dispersed *T. usneoides*, the occurrence in central Chile may be the result of long distance dispersal or a relictual population of a former continuous distribution. Molecular studies of populations from Chile and adjacent regions of Argentina, Bolivia and Peru probably will develop hypotheses for the biogeographic relations and history of this species.

Conservation

According to the Chilean conservation and forestry authority Corporación Nacional Forestal (CONAF), Chile has an area of 143,348 km^2 protected as National Park (Parque Nacional) or National Reserve (Reserva Nacional; CONAF 2008; Fig. 7). Bromeliads, especially the large Puyas ("chaguales") are characteristic elements of central Chilean landscapes and vegetation, and are often perceived as occurring in virtually infinite numbers. This may be true for a few species, but intensive cultivation and construction activities may soon make even these taxa vulnerable. As can be seen in Fig. 7, areas of high bromeliad species richness in Chile lie well outside the protected areas of the country. Moreover, areas of high bromeliad diversity are mainly found in regions that are considerably impacted by man and are densely populated or intensively cultivated.

Other species are very restricted in distribution or extremely rare and thus endangered or even in danger of extinction. For their conservation (*T. tragophoba*, *P. boliviensis*, *T. geissei*, *P. gilmartiniae*, *G. pearcei*, *G. landbeckii*), creating reserves to protect the flora and vegetation in these very restricted areas appears to be the best course of action. As observations of Pinto et al. (2006) reveal, tillandsiales seem to decrease in area obviously not as a result of direct human impact but most probably due to decrease of (fog) humidity. Especially for the restricted, probably relictual distribution areas of the bromeliads in northern Chile, monitoring the stands of the tillandsiales and of the populations of *P. boliviensis*, *T. tragophoba* and *D. chrysantha* seems worthwhile as these taxa can serve as indicators for the development of the unique lomas vegetation.

The endemic species of Robinson Crusoe Island have already found considerable attention and are being protected through conservation efforts. Ex situ conservation is reported for *O. elegans* and *G. berteroi* and should be taken also into account for other species especially when protected areas are close by. The Jardín Botánico Nacional in Viña del Mar for example has an impressive collection of bromeliads (*P. boliviensis*, *P. coerulea* var. *intermedia*, *P. coerulea* var. *violacea*, *O. elegans*, *O. carnea*, *O. litoralis*). The garden is also responsible for a reserve in its vicinity with fine sclerophyllous shrub and impressive populations of *P. chilensis* and *P. berteroniana*. Additionally, the young Botanic Garden "Jardín Botánico Chagual de Santiago" on the outskirts of Santiago, dedicated to the conservation of the native Chilean flora, pays special attention to conservation and propagation of local *Puya* species (Echenique et al. 2003; Muñoz-Schick 2003). Although both gardens focus on the same species, it appears to be important to build a network of such reserves to make sure that efforts not only conserve the diversity of presently recognized species but also the considerable intraspecific genetic diversity. Obviously groups like *P. chilensis* are far more diverse than previously realized and seem to comprise several infraspecific taxa or even species.

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