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Historical assembly of Zygophyllaceae in the Atacama Desert

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Abstract

The Atacama Desert harbors a unique arid-adapted flora with a high degree of endemism, the origin of which is poorly understood. In the Atacama Desert, Zygophyllaceae is represented by five endemic species: one member of Zygophylloideae: *Fagonia chilensis*; and four members of Larreoideae: *Bulnesia chilensis* and *Porlieria chilensis*, the only representatives in the Atacama Desert of genera with disjunct distributions between Argentina, Peru and Chile; and monotypic endemic genera *Metharme lanata* and *Pintoa chilensis*. Zygophyllaceae are thus a particularly suitable group for studying the historical assembly of the Atacama Desert flora as each of these species may represent independent biogeographical events. We made use of published as well as original plastid DNA sequences (*rbcl*, *trnL-trnF* & *trnS-trnG*) to reevaluate the phylogenetic relationships of the Atacama Zygophyllaceae. Bayesian divergence time estimates as implemented in BEAST2 and ancestral area reconstruction with the Dispersal Extinction Cladogenesis approach using BioGeoBEARS were applied to infer ancestral ranges. We compiled the most complete data set of Larreoideae to date with 25 of 28 species. *Bulnesia rivas-martinezii* from Bolivia forms a clade with *Pintoa chilensis* from the Atacama Desert, rendering the genus *Bulnesia* paraphyletic. Most representatives of Zygophyllaceae colonized the Atacama Desert during the Miocene, and only *Fagonia* dispersed more recently. The colonization history of the Atacama Desert in South America is reflected by three individual distribution patterns or floristic elements. The presence of *Bulnesia*, *Pintoa*, and *Metharme* is best explained by Andean vicariance, while the southern Atacama Desert representative, *Porlieria chilensis*, has a continuous distribution into central Chile from where it probably dispersed further north. The only South American *Fagonia* species (*F. chilensis*) likely colonized the Chilean-Peruvian Coastal Desert via long distance dispersal from North America.

Highlights:

- The most comprehensive phylogeny of Larreoideae (Zygophyllaceae) is here presented, including all taxa native to the Atacama Desert and only three missing species.
- The five endemic Atacama Zygophyllaceae species are the result of individual colonization events rather than a single one followed by in-situ diversification.
- The colonization of the Atacama Desert by *Fagonia* is likely the result of long-distance dispersal from North America.
- The colonization of *Bulnesia*, *Pintoa*, and *Porlieria* is probably the results of individual vicariance events and can be linked to the Andean uplift.
- In contrast to several species rich Atacama plant groups, which are mostly annuals, short-lived perennials or shrubs, woody taxa like Zygophyllaceae failed to diversify in the Atacama Desert. This is in contrast to the recent diversification of old world Zygophyllaceae, indicating a low carrying capacity as well as an increased extinction rate for such life forms in this hyperarid environment.

Keywords:

Andes, arid environments, *Bulnesia*, Chile, Historical biogeography, Larreoideae, *Metharme*, South America

Introduction

Located in northern Chile, the Atacama Desert ranges from 18° S at the border region to Peru and 30° S around La Serena, while it is restricted in the east by the Andean mountain range and the Pacific Ocean to the west. Relative to its area, the Atacama Desert is surprisingly species-rich, harboring about 550 species, of which 60% are endemic (Dillon and Hoffmann 1997). However, diversity is not equally distributed in the Atacama Desert. In its northern portion (approx. 18° to 26° S), most species can be found along the coastal range as well as along the Andean foothills, while only few species can survive the harsh conditions of the inner core of the Atacama Desert. Further south, the vegetation is more broadly distributed: whereas the conditions are still predominantly arid, Andean and coastal ranges are not separated by a barren zone (Villagrán et al. 1983, Rundel et al. 1991, Luebert and Pliscoff 2017).

The historical assembly of the Atacama Desert flora has been linked to the timing of the major factors controlling its aridity (Rundel et al. 1991). Recent evidence suggests that the age of aridity can be dated back to the Miocene or even Oligocene (Dunai et al. 2005). However, we still lack a detailed knowledge of the process, since an understanding of the timing of the onset of aridity remains elusive (Ritter et al. 2018), and only few studies have addressed the timing of diversifications of Atacama Desert plant groups (e.g., Luebert and Wen 2008, Dillon et al. 2009, Heibl and Renner 2012, Böhnert et al. 2019).

Zygophyllaceae are key elements of world desert and semi-desert ecosystems, and their diversification is thought to be linked with increased aridity during the Oligocene-Miocene transition, especially in Zygophylloideae (Bellstedt et al. 2012, Wu et al. 2015, 2018). The family has a worldwide distribution, but it is largely restricted to hot and dry regions. Five native genera of Zygophyllaceae are documented for the Atacama Desert, making it one of the Atacama groups with the highest phylogenetic diversity, although each genus is only represented by a single species. The genera *Bulnesia* Gay, *Metharme* Phil. ex Engler, *Pintoa* Gay, and *Porlieria* Ruiz & Pav. belong to the New World endemic Larreoideae, only *Fagonia chilensis* Hook. & Arn. belongs to the sub-cosmopolitan Zygophylloideae. *Bulnesia* and *Porlieria* comprise four species each (Palacios and Hunziker 1984, Godoy-Bürki et al. 2018), while *Metharme* and *Pintoa* are monotypic (Beier et al. 2003).

Understanding the historical assembly of a flora requires evidence for the spatial and temporal origin of its component plant lineages. Based on a review of the distribution and phylogenetic relationships of 53 plant taxa in the Atacama Desert and their closely related species, Luebert (2011) recognized four distribution patterns or floristic elements: (1) tropical Andean, (2) central Chilean, (3) trans-Andean disjunct, and (4) amphitropical disjunct. The two first elements represent species with closely related taxa distributed immediately north or south of the Atacama Desert, pointing to direct floristic exchanges between the

Atacama Desert and its neighboring regions. Disjunct trans-Andean elements, with species distributed on both sides of the Andes, are likely the result of vicariance due to Andean uplift or of trans-Andean dispersal. American amphitropical disjunctions are explained as the result of long-distance dispersal (LDD) events between North and South America (Simpson et al. 2017).

All four floristic elements appear to be present among the five representatives of Zygophyllaceae in the Atacama Desert. *Bulnesia chilensis* Gay, *Pintoa chilensis* Gay, and *Porlieria chilensis* I.M. Johnst. are found in the southern portion of the Atacama Desert, with *Porlieria chilensis* ranging into central Chile. *Metharme lanata* Phil. ex Engl. in turn is found at the dry limit in the northern part of the Atacama Desert. According to Lia et al. (2001) and Godoy-Bürki et al. (2018), *Bulnesia*, *Pintoa*, and *Porlieria* have closely related species on the eastern side of the Andes in Argentina and Bolivia but also in the tropical Andes and the Peruvian coastal desert, respectively. For these genera, if a trans-Andean distribution due to vicariance driven by Andean uplift is to be supported, we expect that each Atacama Desert species is sister to a species distributed on the eastern side of the Andes, and the split between those two sister species coincides with the timing of the Andean uplift. We also expect that floristic exchanges between the Atacama Desert, the tropical Andes, and central Chile are relatively more recent, as suggested in previous works of other taxa (Schwarzer et al. 2010, Gengler-Nowak 2002). South American *Fagonia* L. (*F. chilensis*) is widespread in the Chilean-Peruvian coastal Desert and has its sister species in SW USA and Mexico, where it is hypothesized to have originated (Porter 1974, Beier et al. 2004). A second American amphitropical disjunction, though not directly related to the Atacama Desert, is *Larrea* Cav., a single species of which is proposed to have colonized SW USA + Mexico from southern South America (Hunziker et al. 1972, Lia et al. 2001). Here we expect that *F. chilensis* is part of a clade of New World *Fagonia* and the split from its closest relative can be dated to the Pliocene, thus supporting the proposed hypothesis of Pliocene LDD colonization of the Atacama Desert.

This study takes previous phylogenetic studies on Zygophyllaceae as the starting point (Godoy-Bürki et al. 2018, Wu et al. 2018). We expand the sampling of South American taxa based on field studies and herbarium material to understand the historical assembly of Zygophyllaceae in the Atacama Desert. To this end, we (1) re-evaluate the phylogenetic relationships within Larreoideae with an expanded taxon sampling, (2) estimate divergence times of the Atacama taxa, and (3) infer their ancestral geographical ranges.

Materials and Methods

Taxon sampling

We compiled a broad taxon sampling of Zygophyllaceae across all five subfamilies and 24 of the 25 accepted genera. Two representatives of the sister family

Krameriaceae were used as the outgroup. Furthermore, we present a nearly comprehensive taxon sampling of Larreoideae, with only three accepted species missing, namely *Gonopterodendron carrapo* (Killip & Dugand) A.C. Godoy-Bürki a narrowly endemic and endangered species from Colombia, as well as *Porlieria arida* Rusby and *Izozogia nellii* G. Navarro (Navarro 1997) from Bolivia. For the genus *Bulnesia* we follow the new generic concept of Godoy-Bürki (2015) and Godoy-Bürki et al. (2018). The sampling of Larreoideae is based on the work of Godoy-Bürki et al. (2018), but complemented by original data from additional taxa from Chile, Peru, and Bolivia. As a result, Larreoideae is represented by 25 out of 28 accepted species (approx. 89%), Zygophylloideae by 76 (approx. 42%), and Morkillioideae by three of the four accepted species. Subfamily Tribuloideae is represented by all six accepted genera, but only eight of the approx. 62 species. A complete taxon list including GenBank accessions, vouchers, and/or associated references are provided in the supplementary material (Table S1).

DNA extraction, amplification and sequencing

Genomic DNA was extracted from silica dried leaf tissue or herbarium specimens using the NucleoSpin Plant II kit (Machery-Nagel, Germany) following the manufacturer's protocol with an increased incubation time of 90 min. Sequences of three plastid DNA regions (*rbcL*, *trnL-trnF*, *trnS-trnG*) were amplified using the primer combinations and polymerase chain reaction (PCR) cycling conditions given in supplementary material Table S2 and Tables S3 - S5, respectively. PCR products were purified through gel extraction using NucleoSpin Gel and PCR Clean-up kit (Machery-Nagel, Germany) following the manufacturer protocol. Sequencing was performed on a 3730XL DNA Analyzer (Applied Biosciences) by a sequencing service. Our sampling includes 132 samples, of which 47 are represented by one, 87 by two and 18 by three markers, resulting in a total of ~ 40% missing sequence information. The results of the Godoy-Bürke et al. (2018) show incongruence between plastid and nuclear datasets. Therefore, we decided not to combine plastid and ITS sequence data in our analyses.

Alignment and phylogenetic analysis

Sequences were edited and manually aligned using PhyDe 0.9971 (Müller et al. 2005). One inversion site of two base pairs (bp) was detected in the *trnS-trnG* alignment, reverse-complemented, and aligned for analysis following Quandt et al. (2003). In the *trnL-trnF* and *trnS-trnG* alignments, eight hotspot regions comprising a total of 111 bp were detected and excluded from the analysis. We defined hotspots as regions in the alignment in which poly-A/T stretches or overlapping microstructural mutations over many nucleotides made it difficult to assess homology accurately (Borsch et al. 2003, Löhne & Borsch 2005, Worberg et al. 2007). The position of these hotspots and the inversion in the alignments is reported in the supplementary material available from the CRC1211 public database (File S1 and S2; see data

availability). Maximum Likelihood (ML) approach was employed to evaluate phylogenetic relationships prior to the dating and ancestral area reconstruction analysis of all Zygophyllaceae and Larreoideae. ML analysis was carried out with RAxML 8.2.10 (Stamatakis 2014) under the GTRCAT substitution model and 1,000 rapid bootstrap replicates, treating every gene region as a single partition. The final ML tree was plotted with the python package toytree (Eaton 2019).

Molecular clock dating

A Bayesian relaxed clock model as implemented in BEAST 2.5.1 (Bouckaert et al. 2014) was used to estimate divergence times within Zygophyllaceae. All species with more than one sample were found to be monophyletic, and we used a reduced dataset compared to the ML alignment – one sample per species except for *Bulnesia retama* (Gillies ex Hook. & Arn.) Griseb., which is disjunct between Argentina and Peru – to set up an XML file in BEAUTI 2.5 (Bouckaert et al. 2014). The three partitions of the cpDNA regions were linked with respect to clock and tree models but unlinked with respect to site model. We used bModelTest (Bouckaert and Drummond 2017) as implemented in BEAST2 instead of defining substitution models for each partition. A relaxed lognormal clock with an estimated clock rate and a birth-death model as tree prior were specified (Drummond et al. 2006, Gernhard 2008). The fossil record within Zygophyllaceae is very sparse (reviewed by Bellstedt et al. 2012), and the few documented fossils cannot be confidently assigned to any member of extant genera. We, therefore, used a secondary calibration approach. In order to test the robustness of our approach we analyzed the data twice with two different calibration schemes. First, four clades were specified as monophyletic but only the stem node of Zygophyllaceae was used as secondary calibration point (calibration scheme 1) with normal prior distributions. Second, we applied age constraints on four nodes (calibration scheme 2) with normal prior distributions (Bell et al. 2010, Wu et al. 2015) (see Table 1). The Markov Chain Monte Carlo (MCMC) was run for 100 million generations, sampling every 10,000 generations. The log file was checked using Tracer1.71 (Rambaut et al. 2018) and Maximum Clade Credibility Tree (MCCT) was produced using TreeAnnotator, summarizing mean heights, excluding a burn-in of 10%, and a posterior probability limit of 0.95 was specified in order to obtain HPD intervals only for nodes with sufficient support. Finally, the R-packages ape 5.0 (Paradis and Schliep 2019), phyloch 1.5-5 (Heibl 2008 onwards), strap 1.4 (Bell and Lloyd 2015), and geoscale 2.0 (Bell 2015) were used in R 3.5.1 (R Core Team 2018) and RStudio 1.1.463 (RStudio Team 2016) to plot and annotate the dated tree. Phylogenetic and dating analysis were conducted on the CIPRES Gateway (Miller et al. 2010).

Ancestral area reconstruction

We employed the Dispersal Extinction Cladogenesis (DEC) approach, described by Ree and Smith (2008) and implemented in the R package

Table 1. Age constraints used for normal prior distribution in the BEAST analyses including mean and sigma values (Mean = node age, Min = minimum age, Max = maximum age).

Clade	Mean	Min	Max	sigma	Source
Zygothylaceae stem node	70	49	88	11	Bell et al. 2010; Wu et al. 2015
Zygothylaceae crown node	60.9	34	90	16.3	Magallón et al. 2015
Larreoideae stem node	54.3	41.1	66.9	7.6	Wu et al. 2015
Zygothylloideae crown node	39.8	29.5	51.8	6.4	Wu et al. 2015

BioGeoBEARS 1.1.1 (Matzke 2013), to evaluate the colonization history and timing of the Atacama Desert, both overall for Zygothylaceae and in particular for Larreoideae. We conducted a two-step DEC analysis, one for the whole of Zygothylaceae on a global scale and one for Larreoideae in the Americas. Due to conceptual and statistical problems (Ree and Sanmartín 2018), we did not use the DEC+j model. We used the time calibrated BEAST2 tree and removed the two outgroup taxa, ending up with 114 terminals from 113 species. We ran both analyses with two sets of assumptions (maximum number of areas sets to two and three) and without dispersal constraints over time, because they likely have little effects on the results (Chacón & Renner 2014). For the former, we categorized every sample in the phylogeny in five geographic groups corresponding to: (A) North and Central America; (B) South America; (C) Africa, the Mediterranean, and the Arabian Peninsula; (D) Asia; and (E) Australia. A subdivision of the Americas into two sub-regions was necessary as the New World *Fagonia* have an amphitropical disjunction. For the latter approach, we extracted the Larreoideae from the same MCCT ending up with 26 terminals from 25 species. Two samples of *B. retama* (from Argentina and Peru, respectively) were included to assess the directionality of this trans-Andean disjunction. We categorized the Americas into five geographical units based on the distributional patterns of Larreoideae: North America (A), and Central America and the Caribbean (B) were separated into two distinct units taking into account the amphitropical disjunction of *Larrea*. We also included the northern part of South America (parts of Colombia and Venezuela) into B due to the occurrence of *Guaiaicum* L. along the coast of northern South American and the disjunct distribution of *Gonopterodendron* (Griseb.) Godoy-Bürki between northern and southeastern South America (C). Further, we separated the Peruvian coastal Desert (D) and the Atacama Desert (E) from the remaining parts of the continent in order to understand possible floristic exchanges between them and southeastern South America (C). The designation of areas for each taxon was based on geographical information derived from Zuloaga et al. (2008), Godoy-Bürki et al. (2018) and GBIF¹. The geographical distribution of each taxon for the two analyses is documented in the supplementary material Tables S6 and S7 and in Godoy-Bürki et al. (2018). The R script used to analyze the ancestral

area and to plot the results on the dated phylogeny is publicly available from the CRC1211-database (see Data availability section) and the GitHub² repository.

Results

Phylogeny and divergence times

The final alignment, including the three plastid DNA regions, encompassed 132 samples corresponding to 115 taxa and had a length of 4,631 bp. The backbone topology in Zygothylaceae was largely congruent between ML and the two BEAST2 analyses, receiving moderate to high bootstrap support (supplementary material Figure S1) and posterior probabilities (Figure 1 and supplementary material Figure S2 and S3). Both calibration schemes resulted in similar trees and divergence times estimations documented in supplementary Table S8. Therefore, only the tree with four calibrated nodes is further described and discussed. New World *Fagonia* incl. *F. chilensis* forms a well-supported clade in both analyses, with a crown node age of 4.71 Ma (95% HPD: 1.4–8.6). The stem node age of Larreoideae and Zygothylloideae was estimated at 52.5 Ma (95% HPD: 42.1–62.1), i.e., early Eocene. The crown node age of Larreoideae was dated to the late Oligocene at 28.6 Ma (95% HPD: 18.8–39.1). Within Larreoideae, the “*Guaiaicum*-clade” (Figure 2) encompasses the genera *Porlieria*, *Gonopterodendron*, *Plectrocarpa*, and *Guaiaicum* with a crown node age of 23.6 Ma (95% HPD: 14.6–33.1). *Porlieria chilensis* is the only species of this clade in the Atacama Desert separated from its sister clade (*P. hygrometra* Peru + *P. microphylla* Argentina) in the late Miocene to early Pliocene (6.2 Ma, 95% HPD: 1.7–11.8). The “*Larrea*-clade”, with a crown node age of 20.1 Ma (95% HPD: 11.9–29.2), comprises the genera *Bulnesia*, *Pintoa*, *Metharme*, and *Larrea*. *Bulnesia chilensis* from the Atacama Desert diverged from its sister group (*B. retama* + *B. schickendantzii* + *B. foliosa*) from Argentina and Bolivia around the Miocene-Pliocene boundary (6.3 Ma, 95% HPD: 3–10.2). The monotypic genus *Pintoa* (*P. chilensis*) and *B. rivasmartinezii* from Bolivia form a clade with a crown node age of 2.2 Ma (95% HPD: 0.49–4.52). This clade is placed as sister to the genus *Bulnesia* with a divergence time estimated at 9.3 Ma (95% HPD: 4.8–14.6). The position of the genus *Metharme* within the “*Larrea*-clade” remains unresolved: in both analyses *Metharme* is sister to the remaining members of this clade, but with low support.

1 <http://www.gbif.org/>

2 <https://github.com/TimBoeh/HistBiogeoZygo>

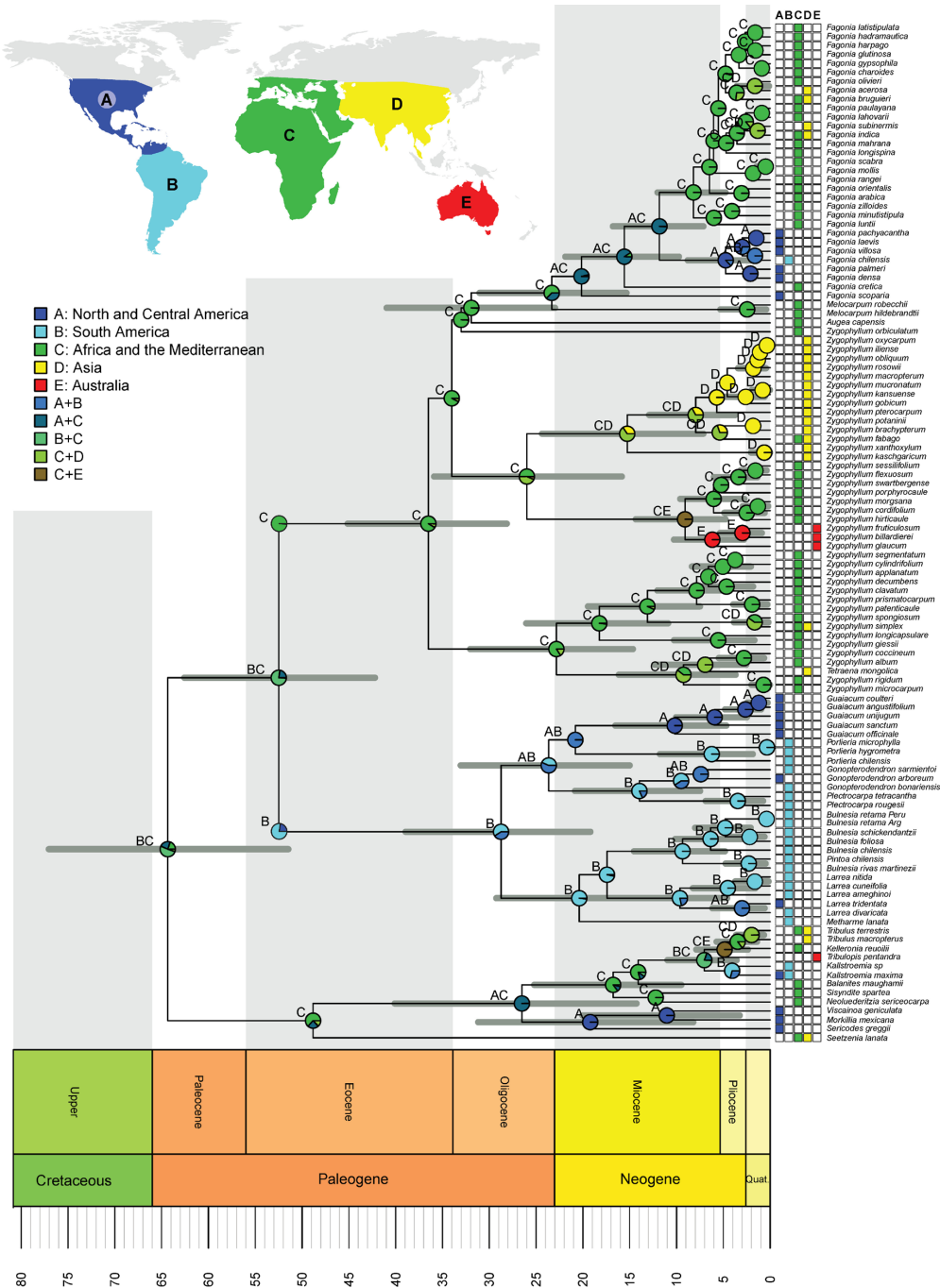


Figure 1. Global ancestral area reconstruction of Zygophyllaceae plotted on BEAST MCCT with outgroups removed and maximum area set to 2 (calibrations scheme 2). Only for nodes with posterior probability support ≥ 0.95 are confidence intervals shown. Squares between tips and tip labels indicate distributions assigned to each single species (A-E), with color codes corresponding to the areas indicated on the map and the legend. Pie charts depict relative probabilities of areas as estimated from the Dispersal Extinction Cladogenesis (DEC) analysis using BioGeoBEARS. Letters next to the pie charts indicate the areas with highest relative probabilities. Pie charts at corner nodes are only given when relevant for interpretation of biogeographic history.

Ancestral area reconstruction

The two ancestral area reconstructions of the whole Zygophyllaceae using two different maximum areas settings are largely congruent, indicating a shared ancestry for the family in South America and Africa, with a first split

of the Tribuloideae, Morkillioideae and Seetzenioideae from Larreioideae and Zygophylloideae during the early Paleocene (Figure 1 & Figure S4). Ancestors of New World *Fagonia* colonized North America from the African-Mediterranean region during the early Miocene and diverged during the middle Miocene. The ancestor

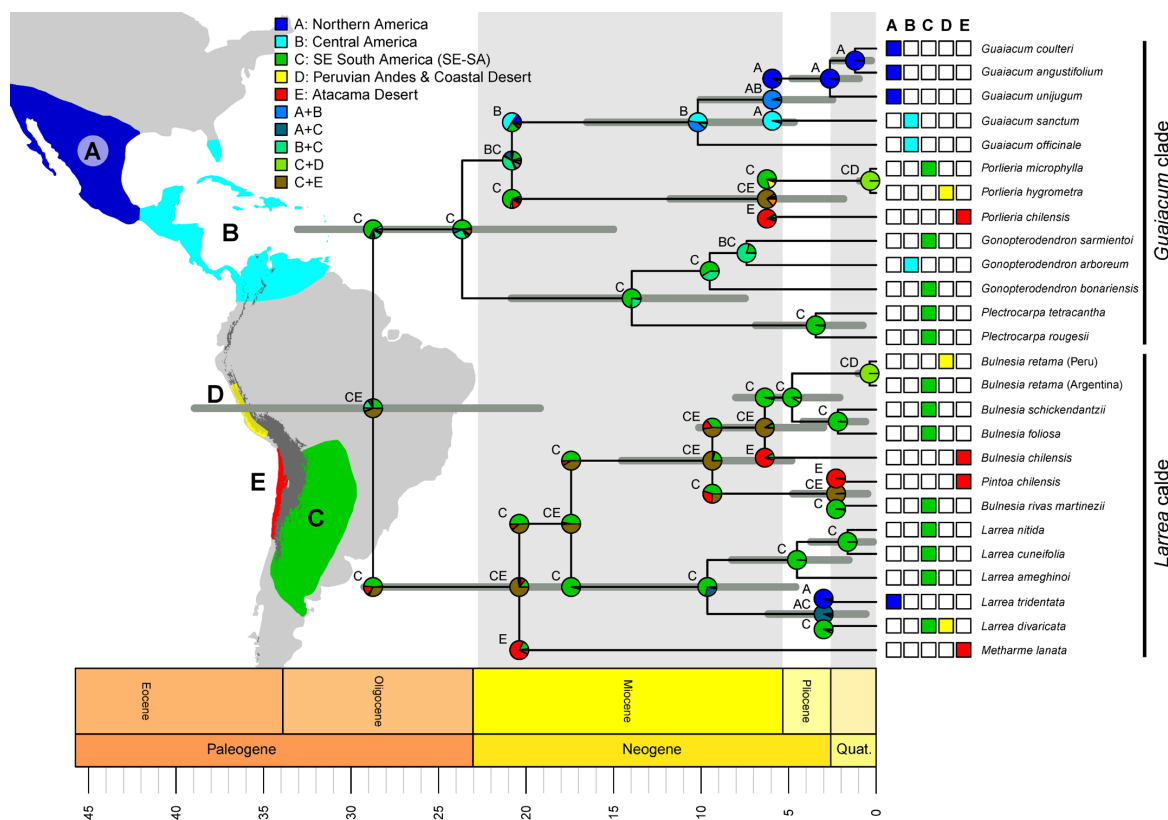


Figure 2. Ancestral area reconstruction of Larreoideae for the Americas plotted on the reduced BEAST tree from Figure 1, with maximum area set to 2 (calibrations scheme 2). Only for nodes with posterior probability support ≥ 0.95 are confidence intervals shown. Squares between tips and tip labels indicate distributions assigned to each single species (A-E), with color codes corresponding to the areas indicated on the map and the legend. Pie charts at the nodes depict relative probabilities of areas as estimated from the Dispersal Extinction Cladogenesis (DEC) analysis using BioGeoBEARS. Letters next to the pie charts indicate the areas with highest relative probabilities. Pie charts at corner nodes are only given when relevant for interpretation of biogeographic history.

of *F. chilensis* subsequently dispersed from North America into South America during the late Pliocene and early Pleistocene. Both ancestral area reconstructions (Figure 2 & Figure S5) indicate that early Larreoideae were likely distributed in South America with at least three subsequent colonization events into northern South America, as well as Central and North America. The analysis of Larreoideae suggests an ancestral area in southeastern South America (SE-SA) + the Atacama Desert during the middle Oligocene. The *Guaiacum* clade has a southeastern South American ancestor with colonizations of Central and North America by *Guaiacum* throughout the Miocene and the arrival of *Gonopterodendron arboreum* in northern South America during the late Miocene. *Porlieria chilensis* and its sister group diverged in the late Miocene from a common ancestor distributed in eastern South America and the Atacama Desert, while the separation of *P. hygrometra* and *P. microphylla* took place < 0.5 mya. In contrast, the second approach (allowing a maximum number of areas of three) points towards a more widespread ancestral range covering eastern South America, the Atacama Desert, and Peru (Figure S5). The *Larrea* clade originated from a common ancestor in eastern South America and the Atacama Desert, with three

independent vicariance events between these areas: one in *Metharme* (early Miocene), one in *Bulnesia* (late Miocene), and one in *Pintoa* (late Pliocene). A recent trans-Andean dispersal into the Peruvian Coastal Desert occurred in *B. retama* coming from east of the Andes.

Discussion

Phylogeny and divergence times in Zygothylaceae

The historical assembly of Zygothylaceae in the New World, and the Atacama Desert in particular, is here analyzed for the first time using a two-step ancestral area reconstruction approach based on plastid data. Dated phylogenies from plastid datasets, as used in this study, are known to produce conflicting results compared to gene trees from nuclear data (Middleton et al. 2014, Vargas et al. 2017). Nuclear phylogenies might provide further insights into the biogeographic history of Zygothylaceae in the Atacama Desert.

Our results are largely congruent with previous phylogenetic analyses of the Zygothylaceae. Only the position of the monotypic Seetzenioidae differs between ML and Bayesian analyses, as previously shown (Sheahan and Chase 2000, Wang et al. 2018, Wu et al. 2018). The time of origin of Zygothylaceae

is estimated to the Cretaceous–Paleogene boundary. At least three colonization events towards the Americas have been identified within Zygophyllaceae: one in each of the subfamilies Morkillioideae, Tribuloideae, and Zygophylloideae. Ancestors of Morkillioideae colonized North America during the late Eocene and members of Tribuloideae (*Kallstroemia* Scop.) in the late Miocene. The last common ancestor of Larreoideae and Zygophylloideae is estimated to have been present in South America and Africa. Wu et al. (2018) proposed a shared ancestry between the New World and Africa, but without separating America into North and South. Approximately 50 Million years ago (early Eocene) the breakup of West Gondwana had already taken place and South America and Africa were no longer connected, though much closer to each other than today (Scotese et al. 1988). An ancient genetically connected population of early Zygophyllaceae with continuous gene flow via stepping stone dispersal distributed in Africa and South America seems possible (Morley 2003). However, an alternative scenario including one or multiple LDD events cannot be ruled out. Further, our expanded dataset supports, under both calibration schemes, that Larreoideae and Zygophylloideae started to diversify in the Miocene as previously suggested by Wu et al. (2018) based on a narrower sampling of Larreoideae. However, our analyses fail to fully resolve the position of monotypic *Metharme*, and the relationships between *Porlieria* and *Guaiacum* remain tentative. The incorporation of *Bulnesia rivas-martinezii* revealed the paraphyly of *Bulnesia* since the species is sister to *Pintoa chilensis* in a clade sister to the remaining species of *Bulnesia*.

Historical assembly of the Atacama Desert flora

The majority of the ~ 35 species of *Fagonia* occur in the Old World and only 8 in the New World (Beier et al. 2004). Our data support the monophyly of New World *Fagonia* and a single LDD event to Central and North America from the Old World followed by a subsequent LDD to South America as previously hypothesized (Porter 1974). However, resolution in this part of the tree is quite limited: as in previous studies, the position of *F. scoparia* remains enigmatic, and according to Beier et al. (2004), a second colonization of North America from the Old World cannot be ruled out. The New World *Fagonia* clade has no internal resolution, making further discussion on biogeographic events inappropriate. Nevertheless, a colonization of the Atacama Desert from north to south within the last 5 Ma seems evident (Simpson et al. 2017).

Among the four representatives of Larreoideae in the Atacama Desert, three have arisen in the desert region in northern Chile during the Miocene (*Bulnesia*, *Porlieria* and *Metharme*) and one during the transition from Pliocene to Pleistocene (*Pintoa*). The most recent common ancestor of *Porlieria* is reconstructed with a distribution in the Atacama Desert and southeastern South America in the late Miocene at a time when the Altiplano-Puna Plateau had already reached elevations above 3000 m (Barnes and Ehlers 2009, Garziona et al. 2014), effectively isolating the eastern and the western

lowlands and suggesting trans-Andean dispersal. However, since the stem lineage of *Porlieria* was distributed in eastern South America, the colonization of the Atacama Desert could have taken place since the Early Miocene. Therefore, Andean vicariance cannot be ruled out. Similar distribution patterns and divergence times estimations are documented for *Bulnesia* and the sister relationship of *B. chilensis* to the remaining species distributed in southeastern South America. These parallel results in *Porlieria* and *Bulnesia* suggest that the progressive Andean uplift during the Miocene led to the isolation of the lineages nowadays distributed on the western and eastern sides of the Andes.

In addition to trans-Andean dispersal and Andean vicariance of closely related taxa (Luebert 2011, Böhnert et al. 2019), Palazzesi et al. (2012) suggested an alternative scenario for the genus *Viviana* (Vivianaceae). Based on pollen records from Patagonia, they hypothesized an origin of the genus in southern South America during the Miocene and a subsequent northward displacement in parallel with increasing aridity during the late Miocene. The Southern and Central Andes would have then acted as a wedge, separating the eastern and western populations and inhibiting gene flow. The highly supported sister relationship between *Pintoa chilensis* and *B. rivas-martinezii* (Figure S1) is an unexpected result of the present study. The divergence time was estimated to 2.2 Ma and requires trans-Andean dispersal and cannot be explained by vicariance due to Andean orogeny (Scott et al. 2018) nor by the northward migration theory proposed for *Viviana* (Palazzesi et al. 2012). The precise position of the peculiar drought-adapted *Metharme lanata* within the *Larrea*-clade as well as its biogeographic history remains elusive, although the placement in that clade is well supported (Godoy-Bürki et al. 2018). However, if *Metharme* in fact dates back to the early Miocene or even to the Oligocene (see HPD intervals in Figure 2), it might be indeed one of the oldest representatives of the Atacama Desert, supporting the “Oligocene-Miocene age of aridity in the Atacama Desert” (Dunai et al. 2005). Clarifying the biogeographic history of *Metharme* requires a phylogenetic analysis with a better-supported placement of *Metharme*.

Recent biogeographic events in Larreoideae

Our results reveal four recent biogeographic events in the Larreoideae. One is the LDD of *Larrea tridentata* to North America. Hunziker et al. (1972) proposed a south-to-north migration for *L. tridentata* based on the assumption that *L. cuneifolia* is “a relatively old” species and sister to the rest of the genus. While the proposed directionality is confirmed, the basis of this assumption is not: *Larrea cuneifolia* diverged from its sister *L. nitida* in the Pleistocene. *L. divaricata* + *L. tridentata* diverged from the remainder of the genus in the late Miocene, parallel to the split between the Atacama endemic *Pintoa chilensis* + Bolivian *B. rivas-martinezii* from the remainder of *Bulnesia*. Porter (1974) argued in favor of a southwards migration of the genus, while in contrast Lia et al. (2001) proposed a late Neogene dispersal of

a diploid ancestor of *L. tridentata* from South America to North America, which agrees with our results of a northwards dispersal during the Pliocene-Pleistocene transition. However, the sister species *L. divaricata* is also found in southern Peru, and we were not able to include a sample from this population in our analysis. The disjunct pattern of *L. divaricata* might parallel the very recent disjunctions in *B. retama* and *Porlieria hygrometra*. *Bulnesia retama* is a xerophytic shrub widely distributed in Argentina from Catamarca in the North to La Pampa in the South, but with an exclave over 1,500 km to the NW in the southern Peruvian coastal region of Ica (Palacios and Hunziker 1984). Our data clearly support a recent dispersal from Argentina into the coastal desert of Peru as proposed by Hunziker (1980). Studies of isozyme variation and DNA content (Poggio et al. 1986, Comas and Hunziker 1996) already suggested a close relationship between these two disjunct metapopulations. Similar distribution patterns as well as timing of dispersal (~ 250K years) are found between the Peruvian *Porlieria hygrometra* from the dry Andean valleys of central Peru and *P. microphylla* from the dry Andean foothills of Argentina and Bolivia. Unfortunately, we were not able to include the fourth species, *Porlieria arida*, from Bolivia. However, those three very recent trans-Andean LDD events are in line with several apparently extremely recent (< 400 years) dispersal events, as argued by Schwarzer et al. (2010). It remains unclear why those groups have not colonized the Atacama Desert in recent times.

Conclusion

There are several plant groups which diversified in the hyperarid Atacama Desert such as *Cristaria*, *Heliotropium*, *Nolana*, and *Oxalis*, all of which represent annual, short-lived perennials or shrubs and mostly go back to single colonizations with relatively short life cycles (Luebert and Wen 2008, Dillon et al. 2009, Heibl and Renner 2012, Böhnert et al. 2019). Conversely, Zygophyllaceae colonized the Atacama Desert five times independently and represents one of the very few families with truly woody representatives in this extreme habitat. Zygophyllaceae, however, entirely failed to diversify in the Atacama Desert – this is in stark contrast to the recent diversification and high species richness of Old World Zygophylloideae (Wu et al. 2015, Lauterbach et al. 2016) or Tribuloideae (Lauterbach et al. 2019). Zygophyllaceae like most other woody genera (e.g., *Balsamocarpon*, *Monttea*, *Prosopis*, *Skytanthus*, *Vasconcellea*, *Huidobria*) only have one or very few species in the Atacama Desert, indicating a relatively low carrying capacity for this life form and/or an elevated extinction rate due to increasing aridity in the Atacama Desert (Rabosky 2013).

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Author contributions

T.B., M.W. and F.L. designed the study. T.B., F.F.M and F.L. carried out fieldwork. T.B., D.Q. and F.L. analyzed the data and T.B., M.W. and F.L. wrote the manuscript and all authors contributed to revision.

Data availability

Additional data including alignments and R scripts are available from the CRC1211-database (<https://crc1211-db.uni-koeln.de>; DOI: <https://10.5880/CRC1211DB.32>).

Declaration of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Supplementary Materials

The following materials are available as part of the online article from <https://escholarship.org/uc/fb>

Table S1. List of species, voucher information and GenBank accession numbers.

Table S2. List of primer for three cp DNA regions used in this study.

Table S3. PCR cycle conditions used to amplify the cp region rbcL.

Table S4. PCR cycle conditions used to amplify the cp region trnL-trnF.

Table S5. PCR cycle conditions used to amplify the cp region trnS-trnG.

Table S6. BioGeoBEARS species distribution matrix for the global Zygophyllaceae dataset.

Table S7. BioGeoBEARS species distribution matrix for Larreioideae dataset.

Table S8. Divergence time estimations for the major nodes of the Zygophyllaceae.

Figure S1. Maximum Likelihood RAXML tree of Zygophyllaceae with Krameriaceae as outgroup.

Figure S2. BEAST2 Maximum clade credibility tree of Zygophyllaceae with Krameriaceae as outgroup and four secondarily calibrated nodes.

Figure S3. BEAST2 Maximum clade credibility tree of Zygophyllaceae with Krameriaceae as outgroup and one secondarily calibrated node.

Figure S4. Global ancestral area reconstruction of Zygophyllaceae plotted on BEAST MCCT with outgroups removed and maximum area set to 3.

Figure S5. Ancestral area reconstruction of Larreioideae for the Americas plotted on the reduced BEAST tree from figure 1 with maximum area set to 3.

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