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Biogeography and conservation status of the pineapple family (Bromeliaceae)

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Abstract

Aim: To provide distribution information and preliminary conservation assessments for all species of the pineapple family (Bromeliaceae), one of the most diverse and ecologically important plant groups of the American tropics—a global biodiversity hotspot. Furthermore, we aim to analyse patterns of diversity, endemism and the conservation status of the Bromeliaceae on the continental level in the light of their evolutionary history.

Location: The Americas.

Methods: We compiled a dataset of occurrence records for 3,272 bromeliad species (93.4% of the family) and modelled their geographic distribution using either climate-based species distribution models, convex hulls or geographic buffers dependent on the number of occurrences available. We then combined this data with information on taxonomy and used the ConR software for a preliminary assessment of the conservation status of all species following Criterion B of the International Union for the Conservation of Nature (IUCN).

Results: Our results stress the Atlantic Forest in eastern Brazil, the Andean slopes, Central America and the Guiana Highlands as centres of bromeliad diversity and endemism. Phylogenetically ancient subfamilies of bromeliads are centred in the Guiana highlands whereas the large radiations of the group spread across different habitats and large geographic area. A total of 81% of the evaluated bromeliad species are *Possibly Threatened* with extinction. We provide range polygons for 3,272 species, as well as newly georeferenced point localities for 911 species in the novel "bromeliad" R package, together with functions to generate diversity maps for individual taxonomic or functional groups.

Main conclusions: Diversity centres of the Bromeliaceae agreed with macroecological patterns of other plant and animal groups, but show some particular patterns related to the evolutionary origin of the family, especially ancient dispersal corridors. A staggering 2/3rds of Bromeliaceae species might be threatened with extinction, especially so in tropical rain forests, raising concerns about the conservation of the family and bromeliad-dependent animal species.

1 | INTRODUCTION

Tropical America (the Neotropics) is a global biodiversity centre comprising the world's largest tropical rain forest and up to one fourth of all plant species (Antonelli & Sanmartín, 2011). Recent studies point to a complex evolutionary history (Hughes, Pennington, & Antonelli, 2013) with geological dynamics (Hoorn, Mosbrugger, Mulch, & Antonelli, 2013; Hoorn et al., 2010; Smith et al., 2014), biotic interactions (Lagomarsino, Condamine, Antonelli, Mulch, & Davis, 2016), and biome connectivity (Antonelli, Zizka, et al., 2018; Zizka, 2019) as causes for the globally outstanding diversity of the region, and point to geological complexity (Antonelli, Kissling, et al., 2018) and current climate (Rangel et al., 2018) as critical to sustain continental-scale diversity patterns.

While recently some progress has been made in providing large-scale distribution information of plant species in the Neotropics (e.g. www.biendata.org; Antonelli, Ariza, et al., 2018), most of the current macroecological and macroevolutionary understanding of the Neotropics at the continental scale is based either on relatively well-studied animal groups, for which standardized distribution information is available ("range maps", www.iucn.org; Guedes et al., 2018; Quintero & Jetz, 2018) or on trees (ter Steege et al., 2013). Despite the crucial importance of non-tree plants for understanding biodiversity and ecosystem functioning, there are still large gaps in the knowledge of their distributions in the Neotropics (Engemann et al., 2015; Feeley, 2015), and scarce and spatially biased knowledge of their distribution is a major obstacle to understanding macroevolutionary and macroecological processes.

The pineapple family (Bromeliaceae) is one of the most species-rich and ecologically important plant families of the Neotropics with 3,503 known species (Butcher & Gouda, 2017). Bromeliads are an abundant and diverse element of many habitats, from the evergreen rain forests of Amazonia to the Atacama Desert. The ecological and evolutionary success of the Bromeliaceae is likely related to the repeated evolution of physiological (e.g. CAM photosynthesis) and morphological (e.g. a tank-like growth and trichomes for water and nutrient uptake via the leaves) key innovations (Crayn, Winter, & Smith, 2004; Silvestro, Zizka, & Schulte, 2014). Approximately 1,552 bromeliad species are epiphytes (WCSP, 2017), mostly in wet tropical forests, and they are often important ecosystem engineers, providing habitat for numerous animal species (Benzing, 2008; Givnish et al., 2011; Versieux et al., 2012).

The Bromeliaceae is virtually endemic to the Americas (one species occurs in West Africa). The family likely originated on the Guiana shield and radiated in the last 20 million years with a subsequent dispersal across the Neotropics (Givnish et al., 2011). Currently, no comprehensive species-level phylogeny of the Bromeliaceae exists, but the taxonomy broadly reflects the evolutionary history of the family with eight subfamilies (Brocchinioideae, Lindmanioideae, Tillandsioideae, Hechtioideae, Navioideae, Pitcairnioideae, Puyoideae and Bromelioideae) forming clades of different ages. The in-situ radiation of Bromeliaceae in the Neotropics, its high diversity, and the adaptation to a wide range of environmental conditions make the family a model to understand the evolutionary history of the Neotropics, and have triggered research interest in its morphology, physiology and diversification (Barfuss et al., 2016; Cáceres, Schulte, Schmidt, & Zizka, 2011; Crayn, Winter, Schulte, & Smith, 2015; Givnish et al., 2011, 2014; Males & Griffiths, 2018; Schuetz, Krapp, Wagner, & Weising, 2016; Silvestro et al., 2014). Yet, no up-to-date treatment of the biogeography of Bromeliaceae exists, and the geographic distribution of many species is poorly known.

This lack of knowledge is especially problematic, since large parts of the Neotropics are under human land use pressure (Soares-Filho et al., 2013). The on-going habitat loss has raised concern that many plant species in the region are threatened with extinction and many of them might go extinct before they are known to science (Lees & Pimm, 2015; ter Steege et al., 2015; Wearn, Reuman, & Ewers, 2012). Scarce resources force a prioritization of conservation effort, often based on the assessment of species' extinction risk, as provided by the Red List of the International Union for the Conservation of Nature (IUCN). However, because IUCN assessments are data intense, plants are often under-represented in the evaluation, especially in poorly studied regions such as the Neotropics. For instance, the IUCN Red List currently only evaluates 240 Bromeliaceae species (6.9%; www.iucnredlist.org). The need to prioritize conservation based on limited data has recently triggered the development of methods for fast, automated conservation assessments, based on a subset of the IUCN criteria using geographic occurrence records only (e.g. Bachman, Moat, Hill, Torre, & Scott, 2011; Dauby et al., 2017; Schmidt et al., 2017). The resulting Automated Assessments (AA) are necessarily coarse but can serve as a data-driven baseline for conservation decisions.

Here, we analyse continental-scale diversity and endemism of the Bromeliaceae and its eight subfamilies. Furthermore, we provide distribution ranges for 3,272 species based on newly compiled geographic data together with an automated conservation assessment based on the geographic distributions. Specifically, we addressed four main questions:

1. *Where are centres of diversity and endemism of the Bromeliaceae?* We expect continental-scale centres of bromeliad diversity and endemism in three regions (Smith, 1934; Smith & Downs, 1974, 1977, 1979): the Andes, a major centre of diversification for many bromeliad genera (Jabaily & Sytsma, 2013; Wagner et al., 2013), the Atlantic Forest in eastern Brazil where especially the subfamily Bromelioideae radiated (Martinelli et al., 2008) and

Central America, where especially the subfamilies Tillandsioideae and Hechtioideae radiated (Givnish et al., 2011). The diversity of bromeliads in the Amazonian lowlands is supposed to be comparatively low, but previous estimates might be biased by a lack of sampling in Amazonia.

2. *How do distinct evolutionary lineages within the Bromeliaceae differ in distribution?* The subfamilies of the Bromeliaceae represent evolutionary coherent groups of different ages and differ in species richness as well as morphological and physiological traits. We expect a larger geographic distribution for the more species-rich subfamilies, related to the evolution of tank habit and CAM photosynthesis in the family.

3. *How many species of Bromeliaceae are threatened with extinction?* Based on the high number of local endemics in the Bromeliaceae (Martinelli et al., 2013, 2008; Wagner et al., 2013) and results from a regional assessments of the Bromeliaceae of Chile (Zizka et al., 2009) and Brazil (Forzza et al., 2013; Martinelli et al., 2013), we expect a relative high number of threatened species compared with other plant families.

4. *Where are hotspots of bromeliad conservation?* Due to the decrease of tropical forest area we expect the epiphytic species to be especially endangered. In contrast, we expect the species of the Andes and the Guiana highlands to be generally less endangered due to lower human land use pressure.

2 | METHODS

We compiled a database of geographic occurrence records for Bromeliaceae from publicly available sources (GBIF.org, 2017, www.idigBio.org, http://splink.cria.org.br, www.tropicos.org) and own fieldwork and databases (data from BN in the Atlantic Forest, from DC in Panama and Costa Rica and from GZ in Chile). For the public databases, we downloaded data on the family level ("Bromeliaceae") and then resolved names on the species level using an up-to-date taxonomic list (Butcher & Gouda, 2017). For those species where we could not obtain occurrences with this procedure, we used Gouda, Butcher & Gouda (cont. updated) to obtain the locality of the type specimen and georeferenced them manually using Google Earth (https://www.Google.com/earth/), if necessary.

Since occurrence records from public databases are error prone (Maldonado et al., 2015), we removed spatial errors following Zizka et al. (2019) and excluded; (a) records without geographic coordinates; (b) records older than 1950, since they are often imprecise due to *post hoc* georeferencing from vague locality descriptions; (c) records based on fossils, tissue samples and living collections; (d) records outside −130 and −20 degrees longitude and above 35 degrees latitude, since the family is endemic to the Americas (we did not include any records for the only West African species *Pitcairnia feliciana*); (e) records with a reported uncertainty higher than 100 km; (f) records flagged as potentially problematic using "CoordinateCleaner v. 2.0-9" (Zizka et al., 2019) in ʀ (R Core Team, 2019), including records in the sea, on country or province centroids, at the locality of

biodiversity institutions, zero coordinates and equal latitude and longitude. Since coordinates assigned to country centroids are a well-known problem (Maldonado et al., 2015), we additionally checked individual localities with many records and manually excluded those localities, if they were close to a country centroid; (g) records outside the botanical country in which a species was registered in the World Check List of Selected Plant Families (WCSP; WCSP, 2017) for those species where these data were available; (h) multiple records of species from individual localities; and (i) for the genus *Vriesea* we additionally verified occurrences based on expert knowledge of BN and AC and excluded records outside the known range of the species.

To address *question 1—patterns of species richness and endemism—*we modelled species ranges using a four-tier approach to overcome the scarce sampling in the study area: (a) for species with $n \geq 15$ records remaining after a spatial thinning using a 25 km nearest neighbour distance with 50 repetitions (Aiello-Lammens, Boria, Radosavljevic, Vilela, & Anderson, 2014), we modelled the distribution based on environmental variables. To do so, we generated pseudo-absences using random sampling within a spatially buffered (500 km) convex hull around the species records (Hijmans, 2017). Then we used an ensemble forecasting using predictions from general additive, random forest and BIOCLIM models weighted by the true skill statistic (TSS; Allouche, Tsoar, & Kadmon, 2006) after model evaluation using k-fold cross-validation ($k = 5$, $n = 4$ random splits; Araújo & New, 2007; Elith & Leathwick, 2009; Guisan, Thuiller, & Zimmermann, 2017). Since the number and sample of pseudo-absences can impact model performance, we replicated the model fitting, sampling two times, eight times and 16 times the number of occurrence as pseudo-absences, with four random replicates, respectively (a total of 12 models per species). For two species (*Aechmea bracteata* and *Hohenbergia stellata*), the models with 16 times the number of pseudo-absences did not converge and we restricted these species to models with two times and eight times the number of pseudo-absences. We then selected the model with the best TSS value for the projection of species' distribution in space (Liu, Newell, & White, 2019). In cases of equal TSS values, we picked the model using less pseudo-absence points. We fitted the models to the first three principal components of 19 bioclim variables from the CHELSA project (Karger et al., 2017), downscaled to 25 × 25 km, using the "sdm v1.0-41" package (Naimi & Araújo, 2016). We restricted the projections to the same buffered convex hull used for sampling the pseudo-absences. We then converted the projected distributions into presence/absence using a threshold of equal specificity and sensitivity (Liu, Newell, & White, 2016) and converted the raster distributions into range polygons. (b) For species with $15 > n \geq 10$ records after filtering and thinning, we followed the same procedure, except that we used only the first two principal components of the climate data. (c) For species with $10 > n \geq 3$ records after filtering, we used a pseudo-spherical convex hull generated with the "speciesgeocodeR v. 2.0-10" package (Töpel et al., 2016) as a representation of the geographic range; and (d) for species with $n < 3$, we used a spatial buffer with 50 km radius (the grain of the diversity analyses) to represent the species range.
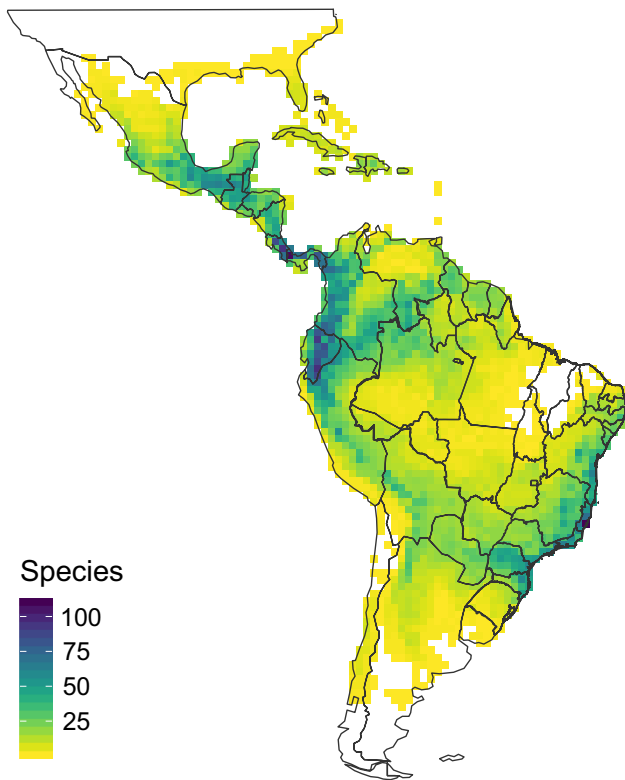
FIGURE 1 The species richness of American Bromeliaceae. Colours indicate the number of species based on modelled ranges. Centres of species richness are the Atlantic Forest in eastern Brazil, the northern Andes and Central America

We overlaid the estimated ranges to visualize species richness patterns for the Bromeliaceae and its subfamilies using the get_range and map_richness function of the novel "bromeliad" package, based on a 100 × 100 km grid. We then used the same grid to estimate the weighted endemism (Crisp & Laffan, 2001) as implemented in R (Guerin, Ruokolainen, & Lowe, 2015) and identified areas of high and low endemism using a significance test based on deviance from the expected endemism, given the observed species richness (Guerin et al., 2015).

To address *question 2—distribution of evolutionary distinct lineages*—we visualized the genus richness and the distribution of the eight subfamilies within the Bromeliaceae. Taxonomic ranks are an imperfect approximation for evolutionary history, but since a species-level phylogenetic tree for the family is missing and the subfamilies likely represent evolutionary clades (Givnish et al., 2011), we used them as proxy for evolutionary history.

To address *question 3—number of threatened species in Bromeliaceae*—we used our database of occurrence records to generate automated conservation assessments (AA) using the "ConR v 1.2.2" package in R (Dauby et al., 2017). ConR calculates the extent of occurrence (EOO), the area of occupancy (AOO) and the number of locations (the latter following a slightly different approach than suggested by the IUCN) for each species based on occurrence records and uses this data to assign each species a threat status following IUCN Red List criterion B ("geographic range", IUCN Standards

& Petitions Subcommittee, 2017). We used the AOO cell size of 4 km^2 as recommended by the IUCN (IUCN Standards & Petitions Subcommittee, 2017). We used raw occurrences rather than the modelled species distributions for the AA, since a reliable AOO estimation as proposed by the IUCN (IUCN Standards & Petitions Subcommittee, 2017) requires a finer grain (2 × 2 km) than our distribution models (25 × 25 km) provide. "ConR" generates AAs in which each species is classified to the standard IUCN Red List categories (Least Concern, Near Threatened, Vulnerable, Endangered and Critically Endangered). We used this detailed AA, to create binary assessment, for which we combined species assessed as Least Concern (*LC*) or Near Threatened (*NT*) as *Not Threatened* and those categorized as Vulnerable (*VU*), Endangered (*EN*) and Critically Endangered (*CR*) as *Possibly Threatened*. Because we aim to set a data-driven baseline for future assessment effort, and because the agreement of the AA with threat search assessments was higher, we focus on this binary assessment throughout the text (See Appendix S2 and Appendix S3 for the individual threat categories of all species). Since AA following Criterion B are based on limited data, we used the ThreatSearch database (https://www.bgci.org/threat_search.php) to compile a reference dataset of existing conservation assessments of Bromeliaceae species from literature to benchmark the quality of our AA. We limited this ThreatSearch reference dataset to assessments with a global scope and the most up-to-date assessment if multiple assessments for a species were available.

To address *question 4—distribution of threatened Bromeliaceae species*—we first visualized the distribution of all *Possibly Threatened* species in a 100 × 100 km grid. Furthermore, we classified each species into 12 major biomes (Olson et al., 2001) to identify the number and fraction of possibly threatened species in each biome. We classified species as present in a biome if at least 5% of its occurrence records were in this biome, since this threshold replicated independent distribution data best (Antonelli, Zizka, et al., 2018).

3 | RESULTS

We obtained 783,975 occurrence records for 16,582 taxa of Bromeliaceae. After geographic cleaning and taxonomic scrubbing, we retained 59,600 records from 3,272 accepted species. Most records were from public databases (55,688 records), mostly GBIF (52,076), based on vouchers (51,831), complemented by data collected by DC, GZ and BN (2,824). Furthermore, we contributed 1,075 occurrence records for 911 species by digitizing and georeferencing the localities of their type specimens. The best sampled species was *Tillandsia recurvata* (L.) L. with 2,433 records, the median number of records per species was 3. A total of 370 species had more than 14 records, 212 species had between 9 and 15 records (hence distributions for 582 species were estimated using niche models); 1,061 species had between 4 and 9 records; and 1,629 species had less than three records. We could not obtain occurrence records for 231 accepted names. Figure S1.1 in Appendix S1 shows the density of occurrence records across the study area.
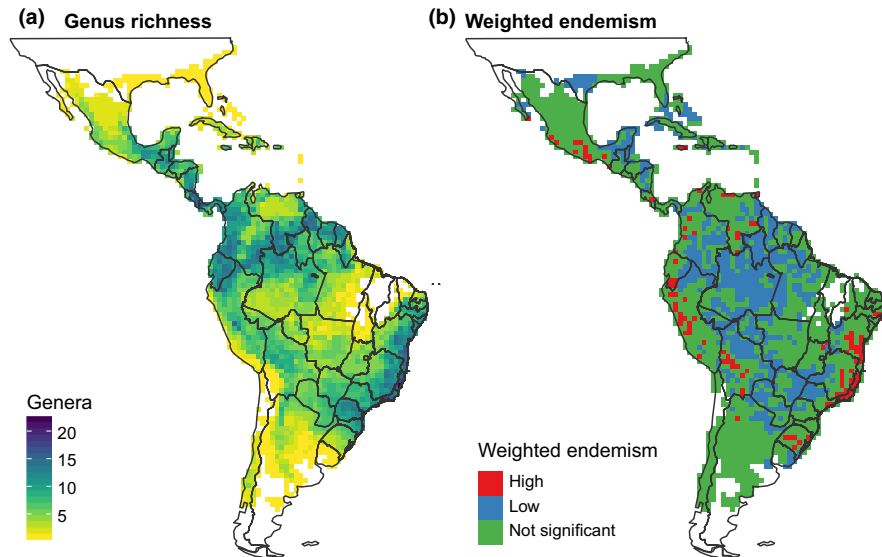
FIGURE 2 Genus richness and weighted endemism of American Bromeliaceae. (a) Genus richness. Colours indicate the number of genera based on modelled ranges. Centres of diversity are the Atlantic Forest in eastern Brazil, the region between Venezuela and Guyana, and the northern Andes. (b) Weighted endemism. Colours indicate if the weighted endemism was higher, lower or not significantly different from the null expectation given the local species richness. Centres of endemism are in the Atlantic Forest, the central Andes, southern Venezuela and southern Mexico. In contrast, most parts of Amazonia and central South America have lower endemism than expected

3.1 | Diversity and endemism

Bromeliaceae species occurred from the southern United States to southern Argentina and Chile (see Appendix S2 for distribution maps of all species). Our results stressed the Atlantic Forest, Central America and the northern Andes as centres of Bromeliaceae diversity (Figure 1). The Guiana shield, the north-western Amazon basin and the area west of the Andes were less diverse. The southernmost USA, northern Mexico, the northernmost part of South America, central and southern Amazonia, the north-east of Brazil, Chile and Peru west of the Andes and Central Argentina had few bromeliad species (see Figure S1.2 for the diversity pattern based on the raw records).

The pattern was different on the genus level, where the Guiana highlands and north-western Amazonia emerged as additional centres of diversity (Figure 2a). The areas with lowest genus diversity were the northern and southern limits of the distribution, the desert areas west of the Andes in southern Peru and northern Chile and the north-eastern part of Brazil (the Caatinga and adjacent Cerrado areas).

The Atlantic Forest in eastern Brazil, the Andes, Central Mexico and parts of Venezuela emerged as centres of high weighted endemism (p < .05; Figure 2b, Figure S1.3). In contrast, large parts of lowland Amazonian and the Cerrado savanna showed significantly lower endemism than expected from the observed species richness (p < .05; Figure 2b, Figure S1.3).

The eight subfamilies differed considerably in their distribution. Of the five smaller subfamilies, two—the Brocchinoideae and the Lindmanioideae—were restricted to the Guiana highlands, and the subfamily Navioideae to the Guiana highlands and adjacent

northern Amazonia. The Hechtioideae was limited to Central and North America and the Puyoideae occurred mostly in the Andes (Figures 3 and 4). Members of the three species-rich subfamilies occurred across the entire range of the family but differed in their diversity centres. The Bromelioideae was most species-rich in eastern Brazil, whereas the Pitcairnioideae and Tillansioideae were most diverse in the northern Andes (Figures 3 and 4).

3.2 | Conservation assessment

The automated conservation assessment (AA) identified 2,638 species (81% of the evaluated species) as *Possibly Threatened* (Table 1, see Appendix S3 for the individual assessment of all species). The percentage of *Possibly Threatened* species varied from 60% in Brocchinioideae to 98% in the Lindmanioideae (Table 2). Interestingly, the percentage of *Possibly Threatened* species also differed among life-forms, with 94% of lithophytic species, 89% of terrestrial species and 74% of epiphytic species classified as *Possibly Threatened* (Table 1). The proportion of possibly threatened species varied among biomes, from 33% in Flooded Savanna and Grasslands to 77% in Tropical and Subtropical Moist Broadleaf Forests (Figure 5). Most of the *Possibly Threatened* species occurred in Tropical and Subtropical Moist Broadleaf Forests (1,928 species) followed by Tropical and Subtropical Grasslands, Savanna & Shrublands (315 species).

The AA yielded information on the threat status of 2,417 species for which no information was available in the ThreatSearch. For those species that had an AA and an assessment in ThreatSearch (n = 786), these agreed in 76.7% of the cases. Of those species for which the assessments disagreed, the AA overestimated threat in 35.1% of the
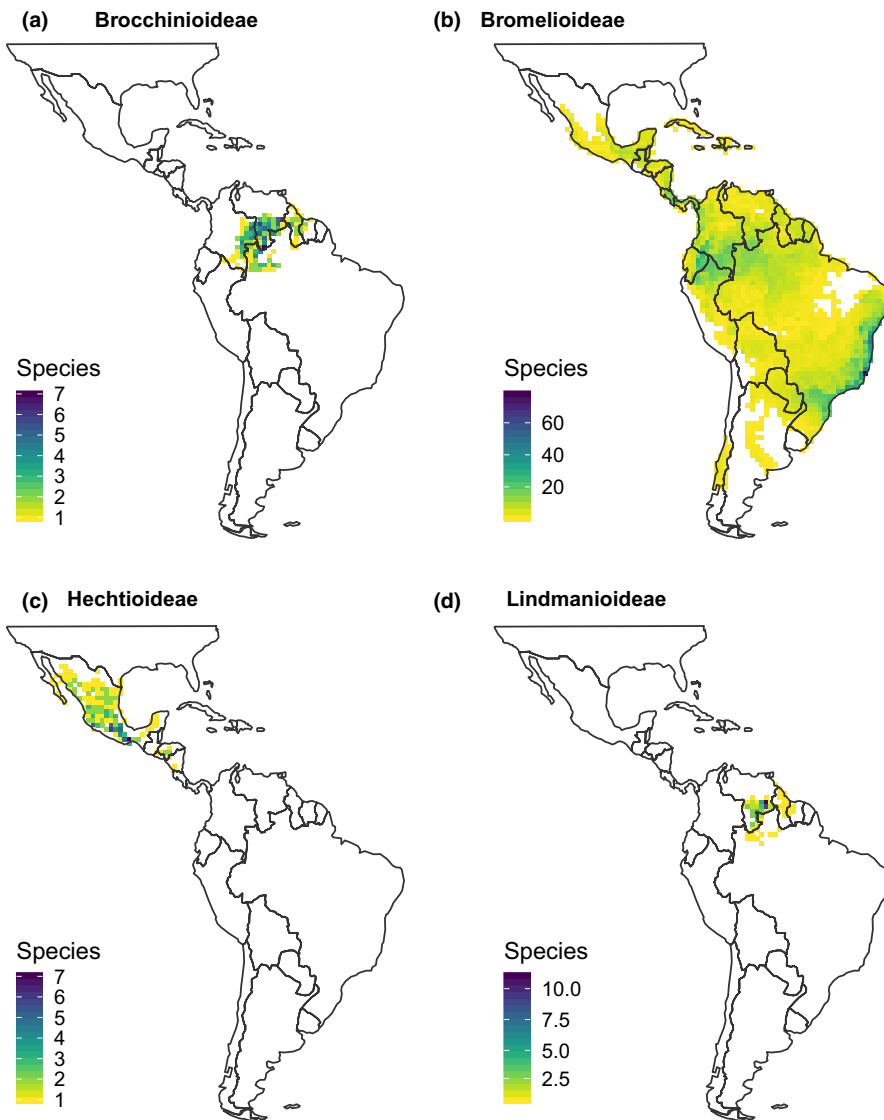
(a) Brocchinioideae

(b) Bromelioideae

FIGURE 3 Species richness of Bromeliaceae subfamilies. The subfamilies differ strongly in their distribution. The Brocchinioideae and Lindmanioideae are restricted to northern Amazonia, and the Hechtioideae to Central and North America, whereas the Bromelioideae occur throughout the range of the family, with high species richness in the Atlantic Forest of eastern Brazil

(c) Hechtioideae

(d) Lindmanioideae

cases (species considered *Not Threatened* in ThreatSearch, but classified as *Possibly Threatened* by the AA) and underestimated threat in 64.9% of the cases (Table 2).

4 | DISCUSSION

Here, we provide modelled distribution ranges for 3,272 species (93.4%) of the pineapple family and identify the Atlantic Forest, the Andes, Central America and southern Venezuela as centres of diversity and endemism of the family. Based on an automated conservation assessment, 2,638 bromeliad species (81% of the evaluated species) were *Possibly Threatened* with extinction, especially in the Atlantic Forest and the Andean slopes.

The results presented here are the first comprehensive treatment of the Bromeliaceae biogeography since Smith and Downs (1974), Smith and Downs (1977) and Smith and Downs (1979), who gave distribution maps for subfamilies and genera in their old circumscription for the then much smaller number of bromeliad species based

on a much smaller dataset. Other previous biogeographic studies in the family had limited taxon and locality sampling (Benzing, 2000; Canela, Paz, & Wendt, 2003; Givnish et al., 2011, 2014; Males & Griffiths, 2018; Smith, 1934; Smith & Downs, 1974, 1977, 1979) and focused on individual taxa (Canela et al., 2003; Leme, Heller, Zizka, & Halbritter, 2017; Peters, 2009; Will & Zizka, 1999; Zizka, Horres, Nelson, & Weising, 1999; Zizka, Trumpler, & Zöllner, 2002) or geographic regions (Cáceres, 2012; Judith et al., 2013; Zizka et al., 2009; www.floradobrasil.jbrj.gov.br). Our distribution maps are available in Appendix S2, and we supply all species ranges under a CC-BY license via the bromeliad R package, which also includes functions for publication-level species richness maps for individual genera, traits or conservation categories (Appendix S4).

We compiled our dataset of geographic occurrence records from publicly available sources subjected to automatic cleaning and manually curated datasets. The dataset is not complete, and we included data based on a compromise between data precision and data availability. To overcome the generally scarce and biased sampling in the Neotropics, we combined multiple range modelling algorithms. While

FIGURE 4 Species richness of Bromeliaceae subfamilies (cont.). The Navioideae are restricted to northern Amazonia, and the Puyoideae are mostly confined to the Andes, whereas the Pitcairnioideae and Tillandsioideae occur throughout the family range, with exceptionally high species richness in the northern Andes
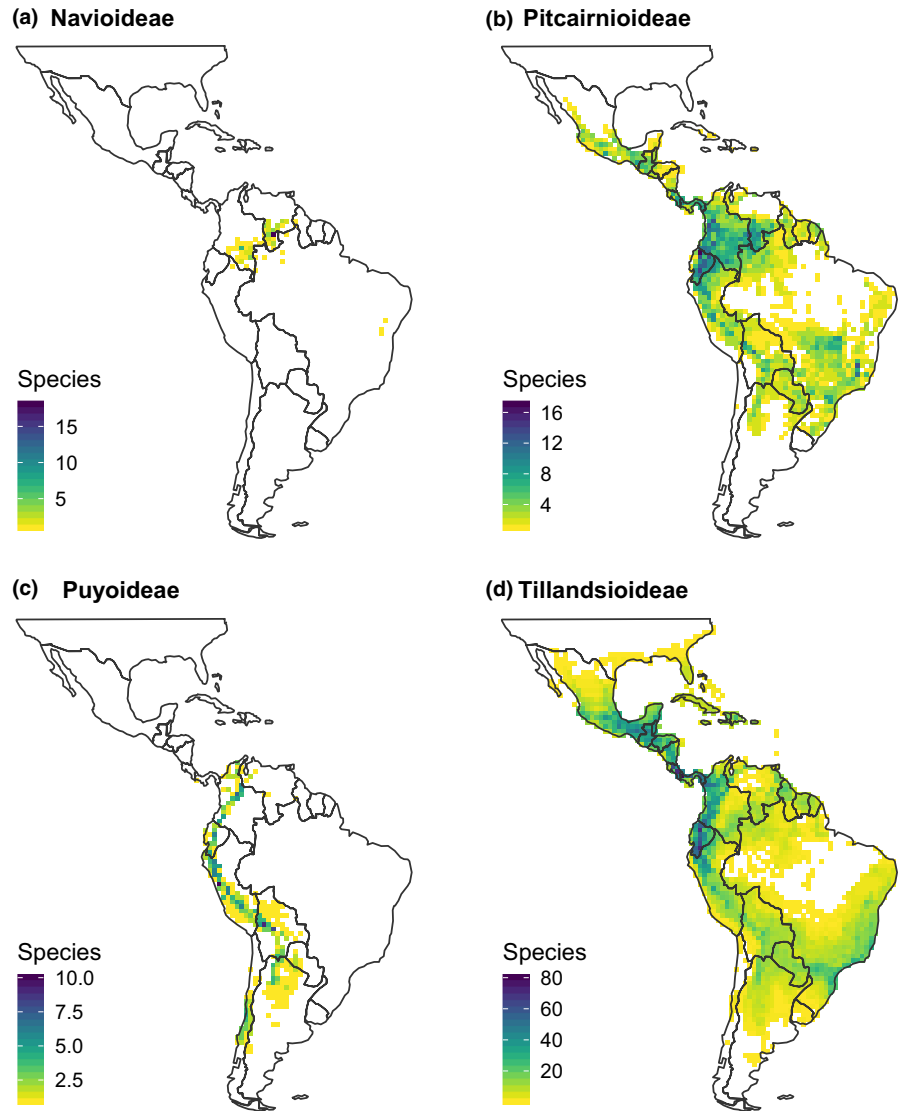
each of these algorithms as well as their combination has limitations, we are confident that our range maps are an adequate representation of Bromeliaceae distribution given the grain of our analyses and enable a comprehensive assessment of the Bromeliaceae biogeography. The openly accessible distribution ranges will serve as a resource to the bromeliad research community and will hopefully enable future studies to relate species distribution to physiological and morphological adaptations in a more detailed manner.

4.1 | Diversity and endemism

The major diversity hotspots we identified—the Atlantic Forest, the northern Andes and Central America (including Southern Mexico)—confirm the centres of diversity identified in previous studies (e.g. Smith, 1934). Novel and noteworthy are two species-rich "corridors", the first extending from the northern Andes over north-western Amazonia (The Napo and Imeri province sensu Morrone, 2014) and the Guiana Highlands to eastern Venezuela and the Guiana Lowlands; and the second one extending from the Andean knee to the Brazilian Atlantic Forest (including the Rondonia, Chacoan,

Atlantic, Parana Forest and Araucaria Forest provinces; Figure 1). These areas correspond to hypothesized dispersal corridors during Bromeliaceae evolution, along which (a) the early bromeliads spread from the Guiana Highlands to the Andes, (b) the early Bromelioideae spread from the Andes to Atlantic Forest, where they underwent their radiation (Givnish et al., 2011; Schulte, Horres, & Zizka, 2005), and (c) important lineages of Tillandsioideae diversified.

Of particular interest are the low-diversity areas in arid northeastern Brazil (the Caatinga and northern Cerrado province), in the central and southern part of the Amazon basin, the Venezuelan Llanos (Sabana province) and the region between the Guiana highlands in the east and the Cordillera de Merida in the north-west. While our modelled distributions should make the results robust to differences in geographic sampling, central Amazonia and the Caatinga and Cerrado are especially poorly sampled (as well as parts of the Atlantic Forest, Feeley, 2015; Werneck, Sobral, Rocha, Landau, & Stehmann, 2011), which might explain part of the observed low species numbers. However, a comparison of our results with local check lists (Holst, 1994, www.floradobrasil.jbrj.gov.br) confirmed that at least the Cerrado, Caatinga and the Llanos are

Taxon	Not threatened	Possibly threatened	Fraction threatened
Family			
Bromeliaceae	633	2,638	0.81
Subfamilies			
Brocchinioideae	8	12	0.6
Bromelioideae	164	732	0.82
Hechtioideae	8	64	0.89
Lindmanioideae	1	43	0.98
Navioideae	3	105	0.97
Pitcairnioideae	75	532	0.88
Puyoideae	17	192	0.92
Tillandsioideae	357	953	0.73
Growth form			
Epiphyte	369	1,026	0.74
Lithophyte	14	208	0.94
Mixed	92	121	0.57
Terrestrial	114	878	0.89

TABLE 1 The number and fraction of *Possibly Threatened* species following an automated conservation assessment split by subfamilies and life form. The fraction of *Possibly Threatened* species is high, especially in the Lindmanioideae and Navioideae. In contrast, the Tillandsioideae and Brocchinioideae, as well as epiphytic species, are less threatened than average

poor in bromeliad species. Hence, the low diversity of these regions might be related to environmental conditions, for instance recurrent fires in the Cerrado and Llanos.

The areas of high Bromeliaceae endemism do not completely overlap with areas of high species richness. While the Atlantic Forest is a centre for species richness and endemism, the diversity centres of the Northern Andes and Central America do not stand out in terms of endemism. Instead, the Central and Southern Andes, southern Mexico and parts of Venezuela emerge as centres of endemism (Figure 2b). A high endemism in the Andes is expected due to the high geological complexity and the related barriers to plant dispersal (Kessous et al., 2019). The area of endemism in southern Mexico corresponds to the distribution of the subfamily Hechtioideae, and the areas in southern Venezuela correspond to the distribution of the subfamilies Brocchinioideae and Navioideae (Figures 3 and 4).

The importance of the Atlantic Forest as centre of Bromeliaceae endemism agrees with studies from other plant groups. In contrast, the other centres of Bromeliaceae endemism are different from those identified for other plant groups. For instance, analyses of all vascular plants species (Kier et al., 2009; Morawetz & Raedig, 2007), the Capparaceae (Mercado Gómez & Escalante, 2019) and the genus *Piper* (Quijano-Abril, Callejas-Posada, & Miranda-Esquivel, 2006) stressed the northern Andes and Central America as centres of endemism for these groups. The different patterns observed in Bromeliaceae might be due to differences in methodology, especially correcting for total species richness, but might also reflect the particular evolutionary history of each group. Interestingly, the low endemism areas we identify for Bromeliaceae, namely lowland Amazonia and Central South America are also low endemism areas for all other groups mentioned above, and correspond to areas of large distribution ranges for rare species (Zizka, Steege, Pessoa, & Antonelli, 2018).

In the absence of a comprehensive species-level phylogeny for the family, the distribution of higher taxonomic ranks might give

TABLE 2 Comparison of the automated conservation assessment of Bromeliaceae species with existing conservation assessments from the ThreatSearch database (https://tools.bgci.org/threat_search.php)

	ThreatSearch	
Automated assessment	Possibly threatened	Not threatened
Possibly threatened	578	46
Not threatened	85	77

some indication of the evolutionary history of the Bromeliaceae (but see Bertrand, Pleijel, & Rouse, 2006). The evolutionary oldest subfamilies (Brocchinioideae and Lindmanioideae) are restricted to eastern Venezuela and the Guianas (Guianan Lowlands province) congruent with the postulated evolutionary origin of the Bromeliaceae in the Guiana highlands (Givnish et al., 2014; Schulte et al., 2005). The distribution of the Hechtioideae corresponds to the known niche preference of this group in dry and seasonal habitats of Mexico (Ramirez-Morillo et al., 2018), with few species extending to the adjacent countries of Central America.

The three most diverse and widely distributed subfamilies, Bromelioideae, Pitcairnioideae and Tillandsioideae reflect the commonly observed "Gentry pattern" (Antonelli & Sanmartín, 2011) with an Andean-centred distribution of the Pitcairnioideae and Tillandsioideae and an Amazonian/Atlantic Forest centred pattern of the Bromelioideae. The bimodal richness pattern of the Pitcairnioideae, with high species richness in eastern South America and in the northern Andes represents the divide of the subfamily into two sister clades (Gomes-da-Silva, Amorim, & Forzza, 2017): the "xeric

FIGURE 5 The distribution of *Possibly Threatened* American Bromeliaceae species. (a) The number of species classified as *Possibly Threatened* by an automated conservation assessment; (b) the proportion of *Possibly Threatened* species per 100 × 100 km gridcell (only cells with five or more species shown); and (c) the number and proportion of *Possibly Threatened* species per biome. The red numbers indicate the fraction of *Possibly Threatened* species in a given biome. Biome names are shortened for better visualization
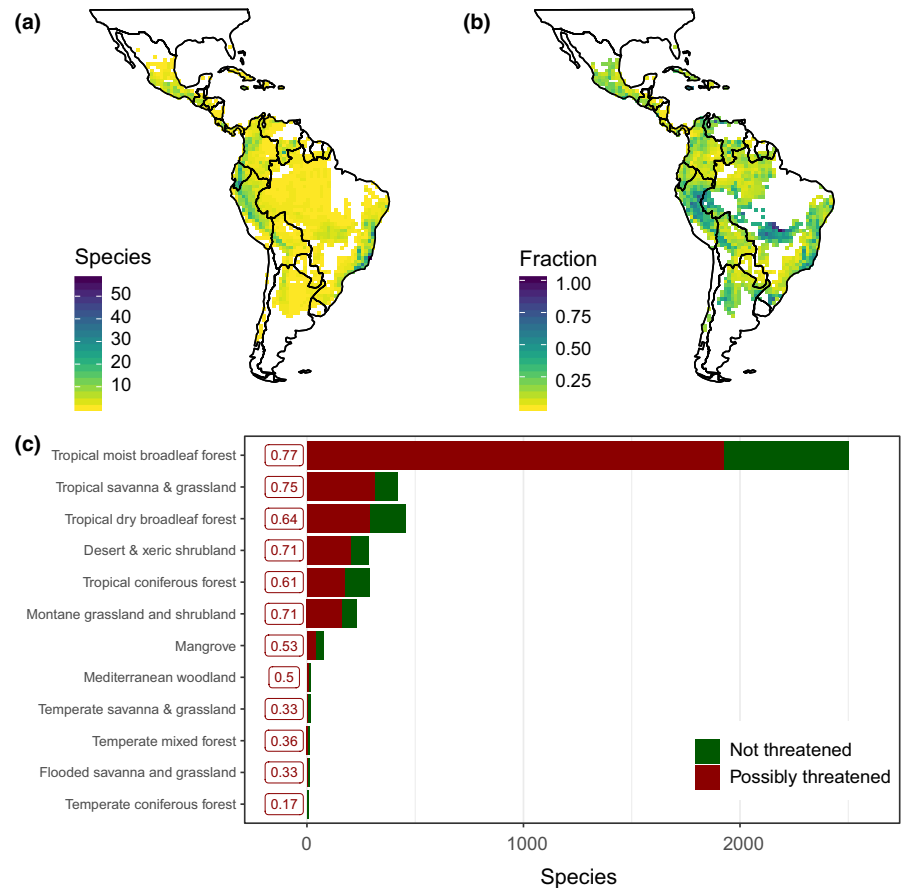
clade" composed by *Dyckia*, *Encholirium* and *Deuterocohnia* in xeric habitats from the central Andes to the Cerrado, Caatinga and Atlantic Forest (Santos-Silva et al., 2013); the clade composed of *Pitcairnia* and *Fosterella* which supposedly originated and radiated in the northern Andes and then colonized the humid and mesic habitats of the northwestern Amazon basin and Central America (Rex et al., 2009, Figure S1.4). The Puyoideae, with the single genus *Puya*, is ecologically well characterized by its Andean distribution, and only few species in this group extend to the Guiana Highlands (*P. floccosa*, *P. grafii*, *P. harrylutheri*, *P. sanctaecrucis*) or Northern and Central Chile west of the Andes (*P. chilensis*, *P. alpestris*, *P. boliviensis*, *P. coerulea*, *P. gilmartiniae*, *P. venusta*) (Jabaily & Sytsma, 2010, 2013; Zizka et al., 2009).

The distribution of individual genera within the Bromeliaceae reflects changes in environmental niche, related to the evolution of key physiological and morphological traits (Males & Griffiths, 2018). For instance, several of the early branching lineages within the subfamily Bromelioideae exclusively comprise species doing C3 photosynthesis (e.g. *Greigia*, *Ochagavia*, *Fascicularia* and *Fernseea*; Crayn et al., 2015), which fits with their distribution in cold to temperate and moist, mostly Andean areas. Contrary to our expectations, the Pitcairnioideae, which are rarely epiphytes (Zotz, 2013) and generally lack key innovations such as tank habit and highly absorptive leaf scales, still have successfully colonized similar ecological and elevation ranges as the Bromelioideae and Tillandsioideae, which did evolve these traits. For part of the Pitcairnioideae, diversification might be linked to other leaf anatomical adaptions to dry environments (Santos-Silva et al., 2013; Saraiva, Mantovani, & Forzza, 2015).

4.2 | Conservation status

Our automated conservation assessment (AA) provides information for 3,032 species for which no full assessment was available from IUCN before. The proportion of 81% of evaluated bromeliad species classified as *Possibly Threatened* seems high compared with the proportion of species considered *Threatened* by the IUCN in other taxonomic groups (around 30%–40% for most taxa). Since AA are mostly based on species range size they might overestimate the threat status of species with few distribution data available (which is the case for many bromeliad species) or of narrow-ranged species without immediate threat, for instance in protected or remote areas. However, the comparison with conservation assessments from the literature shows that our AA in 76.7% of the cases accurately identifies species as *Possibly Threatened* or *Not Threatened*. Furthermore, a regional assessment of the Bromeliaceae of Chile classified a similar proportion (78%) of species as *Threatened*.

In contradiction to our expectation, the proportion of endangered species was higher in terrestrial and lithophytic species than in epiphytes, suggesting that the conservation of habitats where terrestrial bromeliads are diverse might especially benefit bromeliad conservation (See Figure S1.5 for species richness patterns of

different growth forms). For instance, the protection of areas in (semi)arid habitats like the Brazilian Cerrado (with c. 20 genera and 260 species; www.floradobrasil.jbrj.gov.br) are urgent.

In summary, the modelled distribution information here confirmed major macroecological patterns in the Bromeliaceae family, including diversity centres in the northern Andes, the Atlantic Forest and Central America including parts of Mexico and revealed centres of endemism in the Atlantic Forest, the Andes, Central Mexico and parts of Venezuela (*question 1*). Different evolutionary lineages in the Bromeliaceae have distinct geographic distributions, related to the breadth of their environmental niches, with the Brocchinioideae, Lindmanioideae and Navioideae restricted to Southern Venezuela and Northern Amazonia, the Hechtioideae limited to drier parts of Mexico, the Puyoideae restricted mostly to the Andes and the Bromelioideae, Pitcairnioideae and Tillandsioideae spread across the Neotropics (*question 2*). We provide distribution maps and shapefiles of species ranges via the "bromeliad" R package upon publication of this study.

We found 81% of the evaluated species as *Possibly Threatened* with extinction (*question 3*) in many cases in agreement with independent reference assessments. The proportion of *Possibly Threatened* species was particularly high for terrestrial species and in the subfamilies Lindmanioideae, Navioideae and Puyoideae. Most *Possibly Threatened* species occurred in the Atlantic Forest and the Central Andes, especially in Tropical rain forests (*question 4*). This high number is worrying, especially because of the ecological keystone role of many bromeliad species. The automated assessment presented here can act as a data-driven baseline to direct more detailed conservation assessment, which might include data on population dynamics and specific threats.

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DATA AVAILABILITY STATEMENT

The scripts for all analysis used in this study are available from zenodo (https://doi.org/10.5281/zenodo.3243425) under a CC-BY 4.0 license. Distribution maps for all species are available from the electronic supplement of this paper. The species range polygons and the occurrence records georeferenced for this study are accessible via the bromeliad R package under the same license (Appendix S5 and https://github.com/idiv-biodiversity/bromeliad; see Appendix S4 for a tutorial on how to use the package and extract data available upon publication).

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Georg Zizka is a botanist with special interest in systematics, phylogeny, evolution, biogeography and conservation of Bromeliaceae.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.