Conservation status of vascular epiphytes in the Neotropics

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Abstract

The Neotropical realm hosts some of the Earth's most species-rich biodiversity hotspots, with vascular epiphytes significantly contributing to this diversity. However, many regions of the Neotropics where epiphytic species of restricted distribution are reported coincide with threatened ecosystems, such as the tropical montane cloud forest. Moreover, epiphytes may be especially vulnerable to land use and climate change impacts due to their dependence on host trees. We assessed the conservation status of vascular epiphytes in the Neotropics for the families that represent over 80% of the global epiphyte diversity (Araceae, Bromeliaceae, Orchidaceae, Piperaceae, and Polypodiaceae) and identified geographical centers of accumulation of threatened epiphyte species. We gathered information from free-access web repositories, specific epiphytic plant databases, and scientific and grey literature. We assessed the extinction risk of 11,446 epiphyte species following IUCN Red List guidelines, using Criterion B (geographic range size). We found nearly 60% (6,721 species) to be threatened, with 1,766 critically endangered (CR), 3,537 endangered (EN), and 1,418 vulnerable (VU). The threatened species are mainly found in the centers of endemism of vascular epiphytes in Central America, the northern Andes, and the Atlantic Forest. Our study emphasises that the centers of threatened species largely coincide with diversity hotspots, highlighting epiphytes as an especially vulnerable group that requires urgent conservation actions.

Introduction

Epiphytes are plant species that germinate and grow non-parasitically on other plants, mostly trees, where they spend their whole life cycle without root contact with the soil; and thus have a close association with host traits and atmospheric climate (Zotz, 2016). Epiphytes contribute about 10% to the global vascular flora (Taylor et al. 2021; Zotz et al. 2021b). They are particularly conspicuous in tropical and subtropical regions, considered among the world's most diverse areas (Mittermeier et al. 1999; Myers et al. 2000), where epiphytes may represent 20–40% of the flora (Taylor et al. 2021). The Neotropics (tropical America) is one of the most diverse biogeographic realms (Zizka 2019; Raven et al. 2020) and is home to 60% of all vascular epiphyte species currently known, represented most prominently in the families Orchidaceae, Bromeliaceae, Araceae, Polypodiaceae, and Piperaceae (Gentry and Dodson 1987; Taylor et al. 2021).

Vascular epiphytes, which represent a substantial proportion of the total biomass in certain forests (Caballero-Rueda et al. 1997; Martínez-Meléndez et al. 2022; Zotz 2016), influence nutrient cycling (Aguilar-Cruz et al. 2022; Benzing and Seemann 1978) and facilitate animal life in the canopy (Richardson et al. 2000; Stuntz et al. 2002). Epiphytes have specific unique morpho-anatomical and eco-physiological traits that allow them to thrive on trees, including foliar trichomes, tank-forming rosettes, poikilohydry, succulence, and CAM photosynthesis, that allow them to thrive on trees (Benzing 1986; Griffiths and Smith 1983; Hietz 2011; Krömer et al. 2007). As epiphytes have no direct contact with the soil, they are strongly coupled with the atmosphere and capture nutrients and water from different types of precipitation (Zotz et al. 2010; Zotz 2016).

Due to their structural dependency, epiphytes are particularly vulnerable to the effects of landscape modification and climate change (Foster 2001; Köster et al. 2009), especially in montane ecosystems (humid montane forests of Central or South America), where these plants are most diverse and abundant at mid-elevations (Cardelús et al. 2006; Krömer et al. 2005). Within the Neotropics, land use change (encompassing forest clearing for agriculture, selective logging, urbanisation, and road construction) is the strongest driver of biodiversity loss (Nakamura et al. 2017; Sala et al. 2000), and epiphytes are one of the first life forms to be affected by deforestation (Sodhi et al. 2008). Moreover, in these montane ecosystems is also where epiphytes are the most affected by climate change (Foster 2001; IPBES 2018; Knight 2022), i.e., through the reduction of the fog belt used as a water source. Because humid microclimates act as a buffer by providing atmospheric water (Werner et al. 2011), any alteration in montane forest ecosystems can lead to a decrease in species numbers of epiphytes due to local extinction and further changes in species composition (Barthlott et al. 2001; Köster et al. 2009; Krömer et al. 2019, 2021; Zuleta et al. 2016).

In tropical montane regions, there is a high prevalence of species with restricted ranges, and a notable abundance of endemic species (Kessler 2002a, b); these plants are more prone to extinction because of their isolation and adaptation to climatically stable environments (Stevens 1989). The vulnerability of these species to disturbance is enhanced by habitat loss or climatic changes, which may be even more pronounced for species distributed in few localities (Christiansen and Fenchel 2012; Schoener and Spiller 1987; Williams et al. 2009). However, adverse effects on epiphytes cannot be viewed in isolation, since any negative impact on epiphytes will similarily affect other components of the forests (Thomsen et al. 2018; Zotz and Bader 2009).

Conservation efforts to preserve ecosystems inhabited by epiphytes, such as the creation and maintenance of protected areas, often focus on sites with a concentration of endemic and threatened species (Mittermeier et al. 1999; Myers et al. 2000). Since conservation efforts are resource-limited, it is critical to know the identity and distribution of the most threatened species. The Red List of the International Union for Conservation of Nature (IUCN) is a prime source for this information, comprising extinction risk assessments for more than 140,000 plant and animal species (at the time of writing). Unfortunately, each extinction risk assessment using the IUCN Red List Categories requires data on range size, abundance, population, and temporal trends, which are only available for a few species. Therefore, not surprisingly, the Red List includes assessments for < 20% of the estimated global vascular flora (57,987 versus an estimated 342,953 flowering plant species; Govaerts et al. 2021). Many of those species considered threatened in the IUCN Red List have not been recorded in any protected area (e.g., see Tabarelli et al. 2005 for the Atlantic Forest and Oliveira et al. 2017 for Brazil).

Assessments at the regional (state) and national (country) levels are accessible for certain taxonomic groups that contain epiphytic species in the Neotropical region (e.g., Armenta-Montero et al. 2015; Krömer et al. 2013, 2019; Millner et al. 2020; Vergara-Rodríguez et al. 2017). Most of these evaluations use IUCN Criterion B, which considers species range size together with its fragmentation, fluctuation, and decline to estimate extinction risk (IUCN 2022b). While full species assessments for the IUCN Red List are timeconsuming and require a thorough assessment process by trained assessors and extensive documentation, the broader and independent application of IUCN criteria using predictive approaches (see Cazalis et al. 2022 for an overview) have been useful in evaluating groups of species simultaneously, which has led to automated assessments at the global scale for 47% of orchid species (Zizka et al. 2021), and continental scale (Neotropics) for 93% of bromeliads (Zizka et al. 2020b), and 98% of the species of the aroid genus *Anthurium* Schott (Reimuth and Zotz 2020).

Despite the above-mentioned efforts, the extent to which epiphytic species are threatened and their specific locations within the Neotropics remains unclear. To better inform protected area planning, we conducted an automated conservation assessment using unique data based on the geographic distributions of the five most representative epiphyte taxonomic groups - Araceae, Bromeliaceae, Orchidaceae, Piperaceae, and Polypodiaceae -, which together account for approximately 80% of all epiphyte species (Zotz et al. 2021b). As a result, we expected high numbers of threatened species concentrated in centres of endemism and highly diverse areas.

Methods

Study area

We focus on the Neotropics following Morrone et al. (2022), who define the Neotropics as the tropical areas of America, including three subregions (Antillean, Brazilian, and Chacoan) and two transition zones (Mexican and South American), and explicitly exclude the southern portion of the Andes based on the taxon-area cladograms of vascular plants and animal taxa (Morrone 2014; Morrone et al. 2022). In addition, southern Florida (Escalante et al. 2013) and northern Mexico (Morrone 2014) were also excluded since they belong to the Nearctic region (Holarctic realm).

Database

We compiled a database of geo-referenced geographic records of species of the five most species-rich families within epiphytes: Araceae, Bromeliaceae, Orchidaceae, Piperaceae, and Polypodiaceae. We retrieved herbarium records from the Global Biodiversity Information Facility (GBIF 2022). This data was complemented with information from other databases such as the Epiphyte Inventory Group EPIG-DB v1 database (Mendieta-Leiva et al. 2020), Atlantic epiphytes (Ramos et al. 2019), Amazonian epiphytes (Araujo et al. 2022), the South American Dry Diagonal Forest Epiphytes database (Flavio N. Ramos, unpublished data), neotropical Araceae (Alejandro Zuluaga, unpublished data), epiphytes of the Sierra Madre of Chiapas (Jimenez-López et al., 2023a), Usumacinta River basin flora (Jiménez-López et al., 2023b), Biovera-Epi (Guzmán-Jacob et al. 2021), Polypodiaceae of America (Michael Kessler, unpublished data), and Marie Selby Botanical Gardens herbarium (Bruce Holst, unpublished data). Furthermore, we included data from the scientific and grey literature published between 1927 and 2021 (Supporting information: supporting method SM1 and Table S1). For Bromeliaceae, we used data from the “bromeliad” package (Zizka et al. 2020a). For Piperaceae, consisting mainly of species of the genus *Peperomia* Ruiz & Pav. (Zotz et al. 2021b), we also included data with reliable identification from iNaturalist (https://www.inaturalist.org/) revised by the group’s expert (Guido Mathieu, pers. comm.). Data sources can be reviewed in the Supporting information: Table S2.

Since records from public databases (e.g., GBIF and iNaturalist) are error-prone (Maldonado et al. 2015; Zizka et al. 2020a), we only selected records from herbarium specimens (as “preserved specimens” and “material samples” in GBIF). We removed common geographic errors with “CoordinateCleaner v. 2.0–20”(Zizka et al. 2018) and records without geographic coordinates. Databases were joined using the biodiversity data cleaning package “bdc v. 1.1.1” (Ribeiro et al., 2022). To avoid data with possible taxonomic issues, we standardised scientific names with the package “LCVP v. 1.0.3” (Freiberg et al. 2020).

Because growth forms are not accurately and consistently specified in GBIF and additional literature, we used EpiList 1.0 to identify holo- and hemiepiphytes (Zotz 2016; Zotz et al. 2021a), but excluded nomadic vines (i.e., climbing plants that do not have an “epiphytic” phase as these never lose contact with the soil; Moffett 2000; Zotz 2013). For Orchidaceae, Bromeliaceae, and Polypodiaceae, we selected only the species listed in EpiList. For Araceae, we used a species list proposed by Alejandro Zuluaga (unpublished data) since EpiList contained some nomadic vines species for this family. For Piperaceae, we used EpiList, the epiphytic species reported in Flora Mesoamericana (Callejas 2020), and two other recent publications of epiphytic species in the family (Jimeno-Sevilla et al. 2018; Vergara-Rodríguez et al. 2017) to include a most up-to-date species list for the family. All modifications to the EpiList are shown in the Supporting information (Table S3). Finally, we removed duplicated records. All analyses were performed using the software R version 4.2.2 (R Core Team 2022).

Current Red List Categories And Preliminary Assessment Of The Conservation Status

We downloaded the conservation assessments for all available vascular epiphyte species from www.iucnredlist.org (IUCN 2022a) using the IUCN API through the “rredlist v. 0.7.0” package (IUCN 2021) to obtain extinction risk categories of already assessed epiphytic species.

We then preliminarily assessed the extinction risk of epiphyte species belonging to the families Araceae, Bromeliaceae, Orchidaceae, Piperaceae, and Polypodiaceae using the package “ConR v. 1.3.0” (Dauby et al. 2017), which simulates an assessment following IUCN criterion B, by calculating the Extent of Occurrence (EOO, a convex hull around known occurrences), approximating Area of Occupancy (AOO, the area of occupied grid-cells) from geo-referenced occurrences and assuming ongoing range reduction in all species. We used a shapefile of Protected Areas of the World (UNEP-WCMC 2022) to include threat levels in the estimation of the locations, assuming that epiphyte populations within protected areas are under a reduced degree of threat (Dauby et al. 2017). Whenever the EOO and the AOO subcriteria lead to different categories, we selected the highest category of extinction risk following IUCN guidelines (IUCN

2022b). We identified the level of risk for extinction in a particular species by categorising it as either Least Concern/Near Threatened (not threatened), Vulnerable -VU-, Endangered -EN-, or Critically Endangered -CR-. We mapped the number of occurrences and the number of threatened species per 1-degree grid cell with the "map.res" function in the "ConR v. 1.3.0" package (Dauby et al. 2017). Finally, we mapped the resulting raster in Quantum GIS v. 3.22 (2022). We emphasise that our automated assessments are preliminary, but are confident that they can provide a data-driven baseline of extinction risk in epiphytes.

Results

Species occurrences

We obtained 1,892,483 occurrence records of vascular epiphytes within the Neotropics. After geographic cleaning and taxonomic scrubbing, we retained 581,848 records of 11,446 epiphyte species: there were 8,097 epiphyte species of Orchidaceae (71% of all species in the dataset), 1,617 (14%) of Bromeliaceae, 675 (6%) of Araceae, 606 (5%) of Polypodiaceae, and 451 (4%) of Piperaceae (see complete species list in the Supporting information, Table S5). GBIF contributed most of the data (41%), followed by the EpIG database (23%) and online sources (12%). Other ten data sources accounted for the remaining 24% of the records.

The analysed set of species was widely distributed throughout the Neotropics, from northern Mexico to southern Brazil and northern Argentina. Most records were from Mexico, Central America, northwestern Andes, Ecuador, and southeast Brazil, while relatively few data were available for northwestern Brazilian Amazonia, the Llanos, and the south of the Neotropical region (Fig. 1). According to our database, areas with more species mostly matched areas with more collections.

Iucn–red List: Current Assessments

Only 4% of the epiphyte species evaluated here (481 vascular epiphyte species) had existing assessments from the IUCN Red List (made between 2003 and 2022; Supporting information, Table S5). The IUCN-RL (2022) reports the extinction risk for 212 (44%) threatened species (28 critically endangered -CR-, 90 endangered -EN-, and 94 vulnerable -VU-), 38 (8%) near threatened species -NT-, 170 (35%) species of least concern (LC), and 61 (13%) species with deficient data (DD; i.e., appropriate data on distribution is lacking). Bromeliaceae and Orchidaceae had the highest number of evaluated species (184 and 181, respectively), whereas, in Araceae, there were 92 species (all belonging to the genus *Anthurium*); in Piperaceae, 20 species (all *Peperomia*), and Polypodiaceae, only four species in three genera (*Campyloneurum*, *Ceradenia*, and *Pecluma*) were currently evaluated. Within bromeliads and orchids, assessed species belong to 12 and 65 genera, respectively.

Conr: Preliminary Assessments

The preliminary conservation assessment identified 4,725 species in the "LC or NT" category. However, there were 6,721 species (nearly 60% of the evaluated species) as possibly threatened according to the IUCN Criterion B: 1,766 (26%) were critically endangered -CR-, 3,537 (53%) endangered -EN-, and 1,418 (21%) vulnerable -VU- (Table 1 and Supporting information, Table S4). Extinction risks were relatively high among Orchidaceae (64%), Piperaceae (54%), and Bromeliaceae (50%), while proportions were lower in Araceae (44%) and Polypodiaceae (33%) (Table 1).

Table 1
Results of a preliminary automated assessment using range size and ConR, the number of epiphyte species assigned to extinction risk categories following Criterion B assuming constant threat, and the proportion of threatened epiphyte species per family. LC: Least Concern, NT: Near Threatened, EN: Endangered, VU: Vulnerable.

Family	LC or NT	CR	EN	VU	Total
Araceae	377	45	164	89	675
Bromeliaceae	808	153	470	186	1,617
Orchidaceae	2,924	1,470	2,686	1,017	8,097
Piperaceae	208	62	126	55	451
Polypodiaceae	408	36	91	71	606
Total	4,725	1,766	3,537	1,418	11,446

The results of our preliminary assessment were consistent with the current Red List categories (supporting information, Table S4) in 222 of the 481 species (46%). A category was assigned for 61 species previously considered as Data Deficient (DD) (9 species in LC/NT, 3 in VU, 25 in EN, and 24 in CR). Discrepancies were found in 198 cases, assigned to a higher (29%) or lower threat category (12%).

Eleven genera accounted for ca. 50% of the threatened species in this study, which belong to Orchidaceae (7 genera; 2,555 species), Bromeliaceae (2; 391), Araceae (1; 283), and Piperaceae (1; 243). *Epidendrum, Stelis, Lepanthes, Anthurium*, *Masdevallia*, and *Pleurothallis* accounted for 34% of all threatened species (Table 2).

Table 2
Genera with the highest number of threatened epiphyte species based on a preliminary automated assessment using range size and ConR, the number of epiphyte species assigned to extinction risk categories following Criterion B assuming constant threat. LC: Least Concern, NT: Near Threatened, EN: Endangered, VU: Vulnerable.

Genus	Family	VU	EN	CR	Threatened
Epidendrum	Orchidaceae	162	331	132	625
Stelis	Orchidaceae	78	267	237	582
Lepanthes	Orchidaceae	63	320	159	542
Anthurium	Araceae	85	155	43	283
Masdevallia	Orchidaceae	42	157	76	275
Pleurothallis	Orchidaceae	52	149	73	274
Tillandsia	Bromeliaceae	48	140	65	253
Peperomia	Piperaceae	55	126	62	243
Vriesea	Bromeliaceae	33	76	29	138
Oncidium	Orchidaceae	31	67	33	131
Acianthera	Orchidaceae	32	59	35	126

The number of epiphyte species in an extinction risk category varied among regions, with many threatened species in Mexico, Central America, and the northwestern Andes. There were also threatened species concentrated in the Napo Moist and Atlantic Forests (Fig. 2). Although the number of threatened species was generally highest in lower latitudes, Central America includes a substantial number of Orchidaceae and Polypodiaceae, the Atlantic Forest was important for Bromeliaceae, and the southwestern Andes for Polypodiaceae and Piperaceae.

Discussion

Our database covers > 60% of the 17,433 epiphyte species recorded for the Neotropics (Taylor et al. 2021). This amount represents more than 10% of the estimated 118,000 vascular plants in the region (Raven et al. 2020). This study reveals that nearly 60% of the evaluated Neotropical epiphyte species are likely under some level of extinction risk. The number of species threatened with extinction may thus be higher in epiphytes than in many other groups for which estimates exist; for instance, threatened species levels were estimated at 11% for legumes, 19% for bryophytes, 16% for pteridophytes, 17% for monocotyledons, 40% for gymnosperms (Brummitt et al. 2015), and ca. 30% for all land plant species (Pelletier et al. 2018). While these numbers have been obtained using different methodologies and our figure needs to be interpreted with caution, since it is based on the automated application of Criterion B, the absolute numbers from our study are alarming, with over 6,700 epiphyte species potentially at elevated risk of extinction. This number could increase further, as our analysis did not include approximately 37% of Neotropical epiphyte species other than the five focal families of this study.

The need for extinction risk assessments of all known plant species at national, regional, and international levels has been emphasised in various studies (Callmander et al. 2005; Cazalis et al. 2022; Miller et al. 2012). However, current assessment rates must be revised to achieve conservation goals such as the Barometer of Life (Bachman et al. 2019). In this context, automated assessments based on digitally available geographic occurrence records could be crucial in identifying species or groups facing the highest extinction risk to focus manual assessments on species most needing them (Zizka et al. 2020a).

Our assessment differs in the current threat categories of more than 50% of the epiphyte species previously classified by the IUCN-RL. Most of these species were classified by us in a higher class (i.e., higher risk). This finding stresses the need for caution in interpreting automated assessments based solely on digitally available occurrence data (Rivers et al. 2011; Zizka et al. 2020b), although with no better alternatives to keep the IUCN-RL updated, these assessments can provide a valid baseline (Rondinini et al. 2014). For instance, other approaches found a similar proportion of species as threatened for instance between 51–84% in a limited sample of 116 orchid species from New-Guinea (Nic Lughadha et al. 2019).

Among the evaluated Neotropical epiphyte families, we found a higher the extinction risk in Bromeliaceae, Orchidaceae, and Piperaceae, with more than 50% of the species in some category of threat, compared to 30–40% in Araceae and Polypodiaceae. Epiphytic species of the latter two families have the widest distribution ranges (Maria Judith Carmona-Higuita et al., unpublished data) probably due to their dispersal type (e.g., fleshy fruits by ornithochory and chiropterochory, spores by anemochory; Cockle 2001; Mayo et al. 1997; Smith 1972) and less specific habitat requirements (Kessler 2010; Peck et al. 1990), whereas bromeliads and orchids are at the other extreme, with the narrowly endemic species occupying small areas due to specific interactions (e.g., dispersal agents, pollinators, and mycorrhiza; Davis et al. 2015; Jacquemyn et al. 2015; Rasmussen and Rasmussen 2009). Nevertheless, Araceae (including terrestrial and climbing species) have been previously reported among the most species-rich and cosmopolitan flowering plants with many endangered species (Baillie et al. 2004), and some regions have a great proportion of threatened species due to major habitat loss (e.g., Krömer et al. 2019).

Most threatened bromeliads are found in the Atlantic Forest in eastern Brazil, where about 90% of local species are endemic (Ramos et al. 2021; Zizka et al., 2020b). This is also a diversification centre for the family (Givnish et al. 2011; Martinelli et al. 2008). Therefore, species with restricted distributions are likely causing the concentration of threatened species in this region.

Our study identifies the Neotropical epiphytic orchids as the most threatened group, with 64% of their species in a risk category, as indicated by a previous global assessment (Zizka et al. 2021). Since orchids are economically important in horticulture, as well as in the pharmaceutical and food industries (Hinsley et al. 2018; Hossain 2011; Liu et al. 2014; Subedi et al. 2013), and also used in cultural and religious celebrations (Jiménez-López et al. 2019c; Solano-Gómez et al. 2010), so many species are locally endangered due to illegal harvesting (Cruz-Garcia et al. 2015; Flores-Palacios and Valencia-Diaz 2007; Jiménez-López et al. 2019a, b; Krömer et al. 2018, 2021). Although the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES 1973) regulates the trade of orchids (Hinsley and Roberts 2018), wild-harvested orchid taxa are still sold globally in domestic markets and the internet, often in massive quantities (Hinsley et al. 2016, 2017; Perdue 2021; Thomas 2006; Ticktin et al. 2020), so there is an urgent need for identifying the most endangered species to prioritise their conservation.

Our study further suggests that the most species-rich genera within the Orchidaceae family are the most vulnerable to extinction, with *Epidendrum* at 62% of their species under threat, *Lepanthes* at 77%, and *Stelis* at 73%. About 50% of *Epidendrum* species are reported as endemics in some Neotropical regions (Central America; Karremans 2021). Pleurothallidinae comprises 44 genera (including *Lepanthes* and *Stelis*) and 5,100 exclusively Neotropical species (Karremans 2016) distributed mainly in the highlands of the northern Andes and Central America, where they are representative elements of the orchid flora and make up most of their species richness (Pérez-Escobar et al. 2017). However, the causes of these high proportions of affected species require further ecological studies since the categorisation is mainly related to their restricted range (Criterion B), and the probability that a given species has a narrow range is influenced by different factors, specifically by taxon-specific traits and by orographical and historical abiotic factors (Kessler 2002b). It is possible that during Pleistocene climate changes, a multitude of fragmentation and isolation events have promoted speciation, especially of these diverse orchid genera, which can maintain relatively small viable populations within small areas (Jost 2004; Müller et al. 2003).

In Piperaceae, the complicated taxonomy may have led to fewer distributional data, probably influencing the estimation of threat categorisation (Mathieu 2007; Mathieu et al. 2015). Among the studied families, it is perhaps the one with the largest taxonomical issues ("herbarium names"; Mathieu 2007). Nevertheless, many endemic species have been reported in southeast Mexico, the Andes, and Amazon regions (de Figueiredo and Sazima 2007; Frenzke et al. 2015; Mathieu 2001–2020; Vergara-Rodríguez et al. 2017), where the main threats are the continued loss and fragmentation of natural habitats, and these species should be considered as a conservation priority.

Extinction risk was not distributed equally across geographic regions in the Neotropics. There were large numbers of possibly threatened species in the areas with high epiphyte richness, which usually are important centres of diversification for the evaluated families, as in southern Mexico, Central America, the Andes, and the Atlantic Forest in eastern Brazil (Givnish et al. 2014, 2015; Pérez-Escobar et al. 2017). However, the primary source of bias in the Red List assessment of the flora is highly variable geographic coverage. Coverage of plants on the Red List broadly reflects overall patterns of plant species richness, which are also reflected in the areas with fewer evaluated species (Bachman et al. 2019). Importantly, regions with high species numbers tend to be less fully sampled than species-poor regions, even with higher total numbers of records (Soria-Auza and Kessler 2008).

These high-diversity regions or "hotspots" are also the ones with the highest pressure by land use change between 2001 to 2020, according to Global Forest Watch (2014). Assessments of epiphyte families in the most diverse regions of the Neotropics, e.g., Colombia (Calderon 2007; García and Galeano 2006) and Brazil (Freitas et al. 2016), mention deforestation, climate change, and illegal trade as the main causes of extinction of orchid and bromeliad species, placing these families among the most vulnerable plant groups in the Neotropical region.

Conclusion

Our findings from a range-based preliminary assessment of species extinction risk suggest that many threatened species are likely concentrated in centers of endemism and highly diverse areas and that a surprisingly large number of epiphyte species may require consideration in conservation strategies. Effective strategies must be developed to support the establishment of nature reserves, which will be necessary to maintain the current diversity of these threatened groups. Achieving this goal will require further studies and mobilising herbarium data. Colombia, Ecuador, Mexico, Brazil, and certain Caribbean islands have the highest vascular epiphyte diversity. Unfortunately, tropical forests are under threat due to ongoing human disturbance, including deforestation and fragmentation. As a result, national and regional conservation assessments are required to improve the precision of our findings. To promote *in situ* protection and *ex-situ* conservation programs, these assessments must be communicated to governments, institutions, and decision-makers responsible for biodiversity conservation. The Neotropics is one of the species-richest regions in the world, and its protection is critical to maintaining global biodiversity.

Declarations

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Author Contributions

Maria Judith Carmona-Higuita, Thorsten Krömer, and Glenda Mendieta-Leiva contributed to the study's conception and design. All authors contributed data for the analysis. Maria Judith Carmona-Higuita performed material preparation, data collection, and analysis. The first draft of the manuscript was written by Maria Judith Carmona-Higuita and reviewed by Thorsten Krömer. All authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data Availability

The dataset of unpublished data generated and analysed during the current study is embargoed temporarily and is available from the corresponding author upon reasonable request. See public and unpublished data sources in Supplementary information, Table S2.

Supplementary Information (SI)

Supporting information is available in the Zenodo repository, DOI: 10.5281/zenodo.7106172. It includes the supporting methods SM1, supporting Tables S1–S5. Script of analyses of the current study, per species and family maps (shapefile, JPEG, and TIFF), and map of the number of occurrences of the five main vascular epiphyte families per 1-degree grid-cell within the Neotropical region are also available under the Zenodo repository, DOI: 10.5281/zenodo.7106172

Competing Interests

Maria Judith Carmona-Higuita declares that she is writing for her educational purposes, as this investigation is part of her master’s thesis. Therefore, the authors have no relevant financial or non-financial interests to disclose.

Ethical approval

Not applicable.

References

1. Aguilar-Cruz Y, García-Franco JG, Zotz G (2022) Litter-trapping tank bromeliads in five different forests: Carbon and nutrient pools and fluxes. Biotropica 54:170–180. https://doi.org/10.1111/btp.13048
2. Armenta-Montero S, Carvajal-Hernández CI, Ellis EA, Krömer T (2015) Distribution and conservation status of *Phlegmariurus* (Lycopodiaceae) in the state of Veracruz, Mexico. Trop Conserv Sci 8:114–137. https://doi.org/10.1177/194008291500800111
3. Bachman SP, Field R, Reader T, Raimondo D, Donaldson J, Schatz GE, Nic Lughadha EN (2019) Progress, challenges and opportunities for Red Listing. Biol Conserv 234:45–55. https://doi.org/10.1016/j.biocon.2019.03.002
4. Baillie J, Hilton-Taylor C, Stuart S (eds) (2004) 2004 IUCN red list of threatened species: a global species assessment. The IUCN Species Survival Commission. IUCN, Gland, Switzerland and Cambridge, UK

5. Benzing DH (1986) The vegetative basis of vascular epiphytism. Selbyana 9:23–43
6. Benzing DH, Seemann J (1978) Nutritional piracy and host decline: A new perspective on the epiphyte-host relationship. Selbyana 2:133–148
7. Brummitt NA, Bachman SP, Griffiths-Lee J, Lutz M, Moat JF, Farjon A, Donaldson JS, Hilton-Taylor C, Meagher TR, Albuquerque S, Aletrari E, Andrews AK, Atchison G, Baloch E, Barlozzini B, Brunazzi A, Carretero J, Celesti M, Chadburn H, Cianfoni E, Cockel C, Coldwell V, Concetti B, Contu S, Crook V, Dyson P, Gardiner L, Ghanim N, Greene H, Groom A, Harker R, Hopkins D, Khela S, Lakeman-Fraser P, Lindon H, Lockwood H, Loftus C, Lombrici D, Lopez-Poveda L, Lyon J, Malcolm-Tompkins P, McGregor K, Moreno L, Murray L, Nazar K, Power E, Tuijtelaars Q, Salter M, Segrott R, Thacker R, Thomas H, Tingvoll LJ, Watkinson S, Wojtaszekova G, Lughadha KNic, E (2015) Green Plants in the Red: A Baseline Global Assessment for the IUCN Sampled Red List Index for Plants. PLoS ONE 10:e0135152. https://doi.org/10.1371/journal.pone.0135152
8. Caballero-Rueda LM, Rodríguez N, Martín C (1997) Dinámica de elementos en epífitos de un bosque altoandino de la Cordillera Oriental de Colombia. Caldasia 19:311–322
9. Calderon E (2007) Orquídeas, primera parte. Libro Rojo. Instituto Humboldt., Bogota, Colombia
10. Callejas R (2020) In: Piperaceae FM (ed) Universidad Nacional Autónoma de México, Instituto de Biología; Missouri Botanical Garden; Natural History Museum (London). [London], México, D.F.: :. [St. Louis, Mo.]
11. Callmander MW, Schatz GE, Lowry PP (2005) IUCN Red List assessment and the Global Strategy for Plant Conservation: taxonomists must act now. Taxon 54:1047–1050. https://doi.org/10.2307/25065491
12. Cardelús CL, Colwell RK, Watkins JE (2006) Vascular epiphyte distribution patterns: explaining the mid-elevation richness peak. J Ecol 94:144–156. https://doi.org/10.1111/j.1365-2745.2005.01052.x
13. Cazalis V, Di Marco M, Butchart SHM, Akçakaya HR, González-Suárez M, Meyer C, Clausnitzer V, Böhm M, Zizka A, Cardoso P, Schipper AM, Bachman SP, Young BE, Hoffmann M, Benítez-López A, Lucas PM, Pettorelli N, Patoine G, Pacifici M, Jörger-Hickfang T, Brooks TM, Rondinini C, Hill SLL, Visconti P, Santini L (2022) Bridging the research-implementation gap in IUCN Red List assessments. Trends Ecol Evol 37:359–370. https://doi.org/10.1016/j.tree.2021.12.002
14. Christiansen FB, Fenchel TM (2012) Theories of populations in biological communities. Springer Science & Business Media
15. CITES (1973) Convención sobre el Comercio Internacional de Especies Amenazadas de Fauna y Flora Silvestres. https://www.cites.org/esp/disc/text.php (accessed 1.1.16).
16. Cockle A (2001) The dispersal and recruitment of Cyclanthaceae and *Philodendron* (Araceae) understorey root-climbing vines. In: Bongers F, Charles-Dominique P, Forget P-M, Théry M (eds) Nouragues, Monographiae Biologicae. Springer Netherlands, Dordrecht, pp 251–264. https://doi.org/10.1007/978-94-015-9821-7_24
17. Dauby G, Stévart T, Droissart V, Cosiaux A, Deblauwe V, Simo-Droissart M, Sosef MSM, Lowry PP, Schatz GE, Gereau RE, Couvreur TLP (2017) ConR: An R package to assist large-scale multispecies

preliminary conservation assessments using distribution data. Ecol Evol 7:11292–11303. https://doi.org/10.1002/ece3.3704

18. Davis BJ, Phillips RD, Wright M, Linde CC, Dixon KW (2015) Continent-wide distribution in mycorrhizal fungi: implications for the biogeography of specialised orchids. Ann Botany 116:413–421. https://doi.org/10.1093/aob/mcv084
19. de Araujo ML, Quaresma AC, Ramos FN (2022) GBIF information is not enough: national database improves the inventory completeness of Amazonian epiphytes. Biodivers Conserv 31:2797–2815. https://doi.org/10.1007/s10531-022-02458-x
20. de Figueiredo RA, Sazima M (2007) Phenology and pollination biology of eight *Peperomia* species (Piperaceae) in semideciduous forests in Southeastern Brazil. Plant Biol 9:136–141. https://doi.org/10.1055/s-2006-924543
21. Escalante T, Morrone JJ, Rodríguez-Tapia G (2013) Biogeographic regions of North American mammals based on endemism: biogeographical regionalisation of North America. Biol J Linn Soc 110:485–499. https://doi.org/10.1111/bij.12142
22. Foster P (2001) The potential negative impacts of global climate change on tropical montane cloud forests. Earth Sci Rev 55:73–106. https://doi.org/10.1016/S0012-8252(01)00056-3
23. Freiberg M, Winter M, Gentile A, Zizka A, Muellner-Riehl AN, Weigelt A, Wirth C (2020) LCVP, The Leipzig catalogue of vascular plants, a new taxonomic reference list for all known vascular plants. Scientific Data 7, 416. https://doi.org/10.1038/s41597-020-00702-z
24. Freitas L, Salino A, Neto LM, Almeida TE, Mortara SR, Stehmann JR, Amorim AM, Guimarães EF, Coelho MN, Zanin A, Forzza RC (2016) A comprehensive checklist of vascular epiphytes of the Atlantic Forest reveals outstanding endemic rates. PhytoKeys 58:65–79. https://doi.org/10.3897/phytokeys.58.5643
25. Frenzke L, Scheiris E, Pino G, Symmank L, Goetghebeur P, Neinhuis C, Wanke S, Samain MS (2015) A revised infrageneric classification of the genus *Peperomia*. (Piperaceae) Taxon 64:424–444. https://doi.org/10.12705/643.4
26. García N, Galeano G (2006) Libro rojo de plantas de Colombia. Volumen 3: Las bromelias, las labiadas y las pasifloras. Instituto Alexander von Humboldt, vol 3. Instituto de Ciencias Naturales de la Universidad Nacional de Colombia, Ministerio de Ambiente, Vivienda y Desarrollo Territorial., Bogotá, Colombia
27. GBIF (2022) GBIF occurrence download for Araceae, Orchidaceae, Piperaceae, Polypodiaceae. https://doi.org/10.15468/DL.AGYDNR
28. Gentry A, Dodson C (1987) Diversity and biogeography of Neotropical vascular epiphytes. Ann Mo Bot Gard 74:205–233
29. Givnish TJ, Barfuss MHJ, Van Ee B, Riina R, Schulte K, Horres R, Gonsiska PA, Jabaily RS, Crayn DM, Smith JAC, Winter K, Brown GK, Evans TM, Holst BK, Luther H, Till W, Zizka G, Berry PE, Sytsma KJ (2011) Phylogeny, adaptive radiation, and historical biogeography in Bromeliaceae: Insights from an eight-locus plastid phylogeny. Am J Bot 98:872–895. https://doi.org/10.3732/ajb.1000059

30. Givnish TJ, Barfuss MHJ, Ee BV, Riina R, Schulte K, Horres R, Gonsiska PA, Jabaily RS, Crayn DM, Smith JAC, Winter K, Brown GK, Evans TM, Holst BK, Luther H, Till W, Zizka G, Berry PE, Sytsma KJ (2014) Adaptive radiation, correlated and contingent evolution, and net species diversification in Bromeliaceae. Mol Phylogenet Evol 71:55–78. https://doi.org/10.1016/j.ympev.2013.10.010
31. Givnish TJ, Spalink D, Ames M, Lyon SP, Hunter SJ, Zuluaga A, Iles WJD, Clements MA, Arroyo MTK, Leebens-Mack J, Endara L, Kriebel R, Neubig KM, Whitten WM, Williams NH, Cameron KM (2015) Orchid phylogenomics and multiple drivers of their extraordinary diversification. Proceedings of the Royal Society B. 282, 20151553. https://doi.org/10.1098/rspb.2015.1553
32. Global Forest Watch (2014)World Resources Institute [WWW Document]. http://www.globalforestwatch.org
33. Griffiths H, Smith JAC (1983) Photosynthetic pathways in the Bromeliaceae of Trinidad: relations between life-forms, habitat preference and the occurrence of CAM. Oecologia 60:176–184. https://doi.org/10.1007/BF00379519
34. Guzmán-Jacob V, Weigelt P, Craven D, Zotz G, Krömer T, Kreft H (2021) Biovera-Epi: A new database on species diversity, community composition and leaf functional traits of vascular epiphytes along gradients of elevation and forest-use intensity in Mexico. Biodivers Data J 9:e71974. https://doi.org/10.3897/BDJ.9.e71974
35. Govaerts R, Nic Lughadha E, Black N, Turner R, Paton A (2021) The World Checklist of Vascular Plants, a continuously updated resource for exploring global plant diversity. Sci Data 8:215. https://doi.org/10.1038/s41597-021-00997-6
36. Hietz P (2011) Ecology and ecophysiology of epiphytes in tropical montane cloud forests. In: Bruijnzeel L, Scatena F, Hamilton L (eds) Tropical Montane Cloud Forests: Science for Conservation and Management. Doi:10.1017/CBO9780511778384.007, International Hydrology. Cambridge University Press, Cambridge, pp 67–76
37. Hinsley A, Lee TE, Harrison JR, Roberts DL (2016) Estimating the extent and structure of trade in horticultural orchids via social media: Social-Media Orchid-Trade Networks. Conserv Biol 30:1038–1047. https://doi.org/10.1111/cobi.12721
38. Hinsley A, Nuno A, Ridout M, John FAVS, Roberts DL (2017) Estimating the Extent of CITES noncompliance among traders and end-consumers; lessons from the global orchid trade: CITES noncompliance among end-consumers. Conserv Lett 10:602–609. https://doi.org/10.1111/conl.12316
39. Hinsley A, Roberts DL (2018) The wild origin dilemma. Biol Conserv 217:203–206. https://doi.org/10.1016/j.biocon.2017.11.011
40. Hossain MM (2011) Therapeutic orchids: traditional uses and recent advances — An overview. Fitoterapia 82:102–140. https://doi.org/10.1016/j.fitote.2010.09.007
41. IUCN (2022a) The “IUCN” Red List of threatened species. https://www.iucnredlist.org
42. IUCN (2022b) Guidelines for using the IUCN Red List categories and criteria. Version 15. Prepared by the Standards and Petitions Committee. IUCN Standards and Petitions Committee

43. IUCN (2021) rredlist. The “IUCN” Red List is a global list of threatened and endangered species. http://apiv3.iucnredlist.org/api/v3/docs (accessed 2.21.22).
44. IPBES (2018) The IPBES regional assessment report on biodiversity and ecosystem services for the Americas. https://doi.org/10.5281/ZENODO.3236252. Zenodo
45. Jacquemyn H, Brys R, Waud M, Busschaert P, Lievens B (2015) Mycorrhizal networks and coexistence in species-rich orchid communities. New Phytol 206:1127–1134. https://doi.org/10.1111/nph.13281
46. Jiménez-López DA, Carmona-Higuita MJ, Mendieta-Leiva G, Martínez-Camilo R, Espejo-Serna A, Krömer T, Martínez-Meléndez N, Ramírez-Marcial N (2023a) Linking different resources to recognize vascular epiphyte richness and distribution in a mountain system in southeastern Mexico. Flora 152261. https://doi.org/10.1016/j.flora.2023.152261
47. Jiménez-López DA, Gallardo-Cruz JA, Véliz ME, Martínez-Camilo R, Méndez C, Solórzano JV, Velázquez-Méndez L, Carabias J, García-Hidalgo G, Peralta-Carreta C, Sánchez-González M, Castillo-Acosta O, Luna-Kamyshev NM, Villaseñor JL, Meave JA (2023b) High vascular plant species richness in the Usumacinta River Basin: a comprehensive floristic checklist for a natural region in the Mesoamerican biodiversity hotspot. Bot Sci 101:1–62. https://doi.org/doi.org/10.17129/botsci.3253
48. Jiménez-López DA, Pérez-García EA, Martínez-Meléndez N, Solano R (2019a) Orquídeas silvestres comercializadas en un mercado tradicional de Chiapas, México. Bot Sci 97:691–700. https://doi.org/10.17129/botsci.2209
49. Jiménez-López DA, Solano R, Peralta-Carreta C, Solórzano JV, Chávez-Angeles MG (2019b) Species richness may determine the income from illicit wild orchid trading in traditional markets in Mexico. Econ Bot 73:171–186. https://doi.org/10.1007/s12231-019-09460-5
50. Jiménez-López DA, Solórzano JV, Vibrans H, Espejo-Serna A, Peralta-Carreta C (2019c) Ceremonial use of bromeliads and other vascular epiphytes in cemeteries of two indigenous communities of Las Margaritas, Chiapas, Mexico. Econ Bot 73:127–132. https://doi.org/10.1007/s12231-019-09445-4
51. Jimeno-Sevilla HD, Vergara-Rodríguez D, Krömer T, Armenta-Montero S, Mathieu G (2018) Five endemic *Peperomia* (Piperaceae) novelties from Veracruz. Mexico Phytotaxa 369:93–106. https://doi.org/10.11646/phytotaxa.369.2.3
52. Jost L (2004) Explosive local radiation of the genus *Teagueia* (Orchidaceae) in the upper pastaza watershed of Ecuador. Lyonia 7:41–47
53. Karremans AP (2016) Genera Pleurothallidinarum: an updated phylogenetic overview of Pleurothallidinae. Lankesteriana 16:219–241
54. Karremans AP (2021) With great biodiversity comes great responsibility: the underestimated diversity of *Epidendrum* (Orchidaceae). Harvard Papers in Botany 26. https://doi.org/10.3100/hpib.v26iss2.2021.n1
55. Kessler M (2002a) Range size and its ecological correlates among the Pteridophytes of Carrasco National Park, Bolivia. Glob Ecol Biogeogr 11:89–102

56. Kessler M (2002b) The elevational gradient of Andean plant endemism: varying influences of taxon-specific traits and topography at different taxonomic levels. J Biogeogr 29:1159–1165
57. Kessler M (2010) Biogeography of ferns, in: Fern Ecology. Edited by Klaus Mehltreter, Lawrence R. Walker, Joanne M. Sharpe. Cambridge University Press, pp. 22–60
58. Knight J (2022) Scientists' warning of the impacts of climate change on mountains. PeerJ 10:e14253. https://doi.org/10.7717/peerj.14253
59. Köster N, Friedrich K, Nieder J, Barthlott W (2009) Conservation of epiphyte diversity in an Andean landscape transformed by human land use. Conserv Biol 23:911–919. https://doi.org/10.1111/j.1523-1739.2008.01164.x
60. Krömer T, Acebey AR, Toledo-Aceves T (2018) Aprovechamiento de plantas epífitas: implicaciones para su conservación y manejo sustentable, in: E. Silva-Rivera, V. Martínez-Valdéz, M. Lascuráin y E. Rodríguez-Luna (Eds.). De la recolección a los agroecosistemas: soberanía alimentaria y conservación de la biodiversidad. Editorial de la Universidad Veracruzana, Xalapa, México, pp. 175–196
61. Krömer T, Acebey AR, Armenta-Montero S, Croat TB (2019) Diversity, distribution, and conservation status of Araceae in the state of Veracruz, Mexico. Ann Mo Bot Gard 104:10–32. https://doi.org/10.3417/2018214
62. Krömer T, Acebey AR, Smith AR (2013) Taxonomic update, distribution and conservation status of grammitid ferns (Polypodiaceae, Polypodiopsida) in Veracruz State. Mexico Phytotaxa 82:29–44. https://doi.org/10.11646/phytotaxa.82.1.3
63. Krömer T, Kessler M, Gradstein SR (2007) Vertical stratification of vascular epiphytes in submontane and montane forest of the Bolivian Andes: the importance of the understory. Plant Ecol 189:261–278. https://doi.org/10.1007/s11258-006-9182-8
64. Krömer T, Kessler M, Gradstein SR, Acebey A (2005) Diversity patterns of vascular epiphytes along an elevational gradient in the Andes. J Biogeogr 32:1799–1809. https://doi.org/10.1111/j.1365-2699.2005.01318.x
65. Krömer T, Viccon-Esquivel J, Gómez-Díaz JA (2021) Efectos antrópicos sobre la diversidad de epífitas vasculares y orquídeas en el centro de Veracruz. In: Viccon Esquivel J, Castañeda Zárate M, Castro R, Cortés, Cetzal Ix W (eds) Las Orquídeas de Veracruz. Editorial de La Universidad Veracruzana, Xalapa, Ver, pp 235–252
66. Liu H, Luo Y-B, Heinen J, Bhat M, Liu Z-J (2014) Eat your orchid and have it too: a potentially new conservation formula for Chinese epiphytic medicinal orchids. Biodivers Conserv 23:1215–1228. https://doi.org/10.1007/s10531-014-0661-2
67. Maldonado C, Molina CI, Zizka A, Persson C, Taylor CM, Albán J, Chilquillo E, Rønsted N, Antonelli A (2015) Estimating species diversity and distribution in the era of Big Data: To what extent can we trust public databases? Glob Ecol Biogeogr 24:973–984. https://doi.org/10.1111/geb.12326
68. Martinelli G, Vieira C, Gonzalez M, Vieira C, Leitman P, Piratininga A, Costa A, Forzza R (2008) Bromeliaceae da Mata Atlântica Brasileira: Lista de espécies, distribuição e conservação.

Rodriguésia 59:209–258

69. Martínez-Meléndez N, Ramírez-Marcial N, García-Franco JG, Cach-Pérez MJ, Martínez-Zurimendi P (2022) Importance of *Quercus* spp. for diversity and biomass of vascular epiphytes in a managed pine-oak forest in Southern Mexico. For Ecosyst 9:100034. https://doi.org/10.1016/j.fecs.2022.100034
70. Mathieu G (2007) Compendium of herbarium names in the genus *Peperomia* (Piperaceae). Nautilus Acad. Books, Zelzate
71. Mathieu G 2001–2020. The internet *Peperomia* reference. http://www.peperomia.net
72. Mathieu G, Vergara-Rodriguez D, Krömer T, Karger DN (2015) *Peperomia* (Piperaceae) novelties from Veracruz State. Mexico Phytotaxa 205:268–276. https://doi.org/10.11646/phytotaxa.205.4.6
73. Mayo SJ, Bogner J, Boyce PC (1997) The genera of Araceae. Kew, Royal botanic gardens
74. Mendieta-Leiva G, Ramos FN, Elias JPC, Zotz G, Acuña-Tarazona M, Alvim FS, Barbosa DEF, Basílio GA, Batke SP, Benavides AM, Blum CT, Boelter CR, Brancalion PHS, Carmona MJ, Carvalho LP, de la Rosa-Manzano E, Einzmann HJR, Fernández M, Furtado SG, de Gasper AL, Guzmán-Jacob V, Hietz P, Irume MV, Jiménez-López DA, Kessler M, Kreft H, Krömer T, Machado GMO, Martínez-Meléndez N, Martins PLSS, Mello R, de Mendes M, Neto AFM, Mortara L, Nardy SR, Oliveira C, de Ana R, Pillaca AC, Quaresma L, Rodríguez AC, Quiel C, Medina S, Taylor E, Vega A, Wagner MS, Werneck K, Werner MS, Wolf FA, Zartman JHD, Zuleta CE, Jiménez-Alfaro D, B (2020) EpIG-DB: A database of vascular epiphyte assemblages in the Neotropics. J Veg Sci 31:1–11. https://doi.org/10.1111/jvs.12867
75. Miller JS, Porter-Morgan HA, Stevens H, Boom B, Krupnick GA, Acevedo-Rodríguez P, Fleming J, Gensler M (2012) Addressing target two of the Global Strategy for Plant Conservation by rapidly identifying plants at risk. Biodivers Conserv 21:1877–1887. https://doi.org/10.1007/s10531-012-0285-3
76. Millner HJ, Bachman SP, Baldwin TC (2020) An assessment of the conservation status of *Restrepia* (Orchidaceae) reveals the threatened status of the genus. Plant Ecol Divers 13:115–131. https://doi.org/10.1080/17550874.2020.1735553
77. Mittermeier RA, Myers N, Mittermeier CG, Robles Gil P (1999) Hotspots: Earth's biologically richest and most endangered terrestrial ecoregions. CEMEX, SA, Agrupacion Sierra Madre, SC
78. Moffett MW (2000) What's "Up"? A critical look at the basic terms of canopy biology. Biotropica 34:569–596. https://doi.org/10.1646/0006-3606(2000)032[0569:WSUACL]2.0.CO;2
79. Morrone JJ (2014) Biogeographical regionalisation of the Neotropical region. Zootaxa 3782:110. https://doi.org/10.11646/zootaxa.3782.1.1
80. Morrone JJ, Escalante T, Rodríguez-Tapia G, Carmona A, Arana M, Mercado-Gómez JD (2022) Biogeographic regionalisation of the Neotropical region: New map and shapefile. Anais da Academia Brasileira de Ciências 94:e20211167. https://doi.org/10.1590/0001-3765202220211167
81. Müller R, Nowicki C, Barthlott W, Ibisch PL (2003) Biodiversity and endemism mapping as a tool for regional conservation planning – case study of the Pleurothallidinae (Orchidaceae) of the Andean rain forests in Bolivia. Biodivers Conserv 12:2005–2024. https://doi.org/10.1023/A:1024195412457

82. Myers N, Mittermeier R, Mittermeier C, da Fonseca G, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403:853–858. https://doi.org/10.1038/35002501
83. Nakamura A, Kitching RL, Cao M, Creedy TJ, Fayle TM, Freiberg M, Hewitt CN, Itioka T, Koh LP, Ma K, Malhi Y, Mitchell A, Novotny V, Ozanne CMP, Song L, Wang H, Ashton LA (2017) Forests and their canopies: achievements and horizons in canopy science. Trends Ecol Evol 32:438–451. https://doi.org/10.1016/j.tree.2017.02.020
84. Nic Lughadha E, Walker BE, Canteiro C, Chadburn H, Davis AP, Hargreaves S, Lucas EJ, Schuiteman A, Williams E, Bachman SP, Baines D, Barker A, Budden AP, Carretero J, Clarkson JJ, Roberts A, Rivers MC (2019) The use and misuse of herbarium specimens in evaluating plant extinction risks. Philosophical Trans Royal Soc B: Biol Sci 374:20170402. https://doi.org/10.1098/rstb.2017.0402
85. Oliveira U, Soares-Filho BS, Paglia AP, Brescovit AD, de Carvalho CJB, Silva DP, Rezende DT, Leite FSF, Batista JAN, Barbosa JPPP, Stehmann JR, Ascher JS, de Vasconcelos MF, De Marco P, Löwenberg-Neto P, Ferro VG, Santos AJ (2017) Biodiversity conservation gaps in the Brazilian protected areas. Sci Rep 7:9141. https://doi.org/10.1038/s41598-017-08707-2
86. Peck JH, Peck CJ, Farrar DR (1990) Influences of life history attributes on formation of local and distant fern populations. Am Fern J 80:126. https://doi.org/10.2307/1547200
87. Pelletier TA, Carstens BC, Tank DC, Sullivan J, Espíndola A (2018) Predicting plant conservation priorities on a global scale. Proceedings of the National Academy of Sciences 115, 13027–13032. https://doi.org/10.1073/pnas.1804098115
88. Perdue RT (2021) Who needs the dark web? Exploring the trade in critically endangered plants on eBay. Am J Criminal Justice 46:1006–1017. https://doi.org/10.1007/s12103-021-09658-1
89. Pérez-Escobar OA, Chomicki G, Condamine FL, Karremans AP, Bogarín D, Matzke NJ, Silvestro D, Antonelli A (2017) Recent origin and rapid speciation of Neotropical orchids in the world’s richest plant biodiversity hotspot. New Phytol 215:891–905. https://doi.org/10.1111/nph.14629
90. Pérez-Escobar OA, Gottschling M, Chomicki G, Condamine FL, Klitgård BB, Pansarin E, Gerlach G (2017) Andean mountain building did not preclude dispersal of lowland epiphytic orchids in the Neotropics. Sci Rep 7:1–10. https://doi.org/10.1038/s41598-017-04261-z
91. QGIS.org,Quantum GIS Development Team
92. Core Team R (2022) R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria
93. Ramos FN, Mortara SR, Elias JPC (2021) Vascular epiphytes of the Atlantic Forest: diversity and community ecology. In: Marques MCM, Grelle CEV (eds) The Atlantic Forest. Springer International Publishing, Cham, pp 133–149. https://doi.org/10.1007/978-3-030-55322-7_7
94. Ramos, F.N., Mortara, S.R., Monalisa-Francisco, N., Elias, J.P.C., Neto, L.M., Freitas,L., Kersten, R., Amorim, A.M., Matos, F.B., Nunes-Freitas, A.F., Alcantara, S., Alexandre,M.H.N., Almeida-Scabbia, R.J., Almeida, O.J.G., Alves, F.E., Oliveira Alves, R.M.,Alvim, F.S., Andrade, A.C.S., Andrade, S., Aona, L.Y.S., Araujo, A.C., Araújo, K.C.T.,Ariati, V., Assis, J.C., Azevedo, C.O., Barbosa, B.F., Barbosa, D.E.F., Barbosa, F.dos R., Barros, F., Basilio, G.A., Bataghin, F.A., Bered, F., Bianchi, J.S., Blum,C.T., Boelter, C.R., Bonnet,

A., Brancalion, P.H.S., Breier, T.B., Brion, C. de T.,Buzatto, C.R., Cabral, A., Cadorin, T.J., Caglioni, E., Canêz, L., Cardoso, P.H.,Carvalho, F.S., Carvalho, R.G., Catharino, E.L.M., Ceballos, S.J., Cerezini, M.T.,César, R.G., Cestari, C., Chaves, C.J.N., Citadini-Zanette, V., Coelho, L.F.M., Coffani-Nunes,J.V., Colares, R., Colletta, G.D., Corrêa, N. de M., Costa, A.F., Costa, G.M., Costa,L.M.S., Costa, N.G.S., Couto, D.R., Cristofolini, C., Cruz, A.C.R., Del Neri, L.A.,Pasquo, M., Santos Dias, A., Dias, L. do C.D., Dislich, R., Duarte, M.C., Fabricante,J.R., Farache, F.H.A., Faria, A.P.G., Faxina, C., Ferreira, M.T.M., Fischer, E., Fonseca,C.R., Fontoura, T., Francisco, T.M., Furtado, S.G., Galetti, M., Garbin, M.L., Gasper,A.L., Goetze, M., Gomes-da-Silva, J., Gonçalves, M.F.A., Gonzaga, D.R., Silva, A.C.G.e, Guaraldo, A. de C., Guarino, E. de S.G., Guislon, A.V., Hudson, L.B., Jardim, J.G.,Jungbluth, P., Kaeser, S. dos S., Kessous, I.M., Koch, N.M., Kuniyoshi, Y.S., Labiak,P.H., Lapate, M.E., Santos, A.C.L., Leal, R.L.B., Leite, F.S., Leitman, P., Liboni,A.P., Liebsch, D., Lingner, D.V., Lombardi, J.A., Lucas, E., Luzzi, J. dos R., Mai,P., Mania, L.F., Mantovani, W., Maragni, A.G., Marques, M.C.M., Marquez, G., Martins,C., Martins, L. do N., Martins, P.L.S.S., Mazziero, F.F.F., Melo, C. de A., Melo,M.M.F., Mendes, A.F., Mesacasa, L., Morellato, L.P.C., Moreno, V. de S., Muller, A.,Murakami, M.M. da S., Cecconello, E., Nardy, C., Nervo, M.H., Neves, B., Nogueira,M.G.C., Nonato, F.R., Oliveira-Filho, A.T., Oliveira, C.P.L., Overbeck, G.E., Marcusso,G.M., Paciencia, M.L.B., Padilha, P., Padilha, P.T., Pereira, A.C.A., Pereira, L.C.,Pereira, R.A.S., Pincheira-Ulbrich, J., Pires, J.S.R., Pizo, M.A., Pôrto, K.C., Rattis,L., Reis, J.R. de M., Reis, S.G. dos, Rocha-Pessôa, T.C., Rocha, C.F.D., Rocha, F.S.,Rodrigues, A.R.P., Rodrigues, R.R., Rogalski, J.M., Rosanelli, R.L., Rossado, A.,Rossatto, D.R., Rother, D.C., Ruiz-Miranda, C.R., Saiter, F.Z., Sampaio, M.B., Santana,L.D., Santos, J.S. dos, Sartorello, R., Sazima, M., Schmitt, J.L., Schneider, G.,Schroeder, B.G., Sevegnani, L., Júnior, V.O.S., Silva, F.R., Silva, M.J., Silva, M.P.P.,Silva, R.G., Silva, S.M., Singer, R.B., Siqueira, G., Soares, L.E., Sousa, H.C., Spielmann,A., Tonetti, V.R., Toniato, M.T.Z., Ulguim, P.S.B., Berg, C., Berg, E., Varassin,I.G., Silva, I.B.V., Vibrans, A.C., Waechter, J.L., Weissenberg, E.W., Windisch, P.G.,Wolowski, M., Yañez, A., Yoshikawa, V.N., Zandoná, L.R., Zanella, C.M., Zanin, E.M.,Zappi, D.C., Zipparro, V.B., Zorzanelli, J.P.F., Ribeiro, M.C., 2019. ATLANTIC EPIPHYTES:a data set of vascular and non-vascular epiphyte plants and lichens from the Atlantic Forest. Ecology 100, e02541. https://doi.org/10.1002/ecy.2541

95. Rasmussen HN, Rasmussen FN (2009) Orchid mycorrhiza: implications of a mycophagous lifestyle. Oikos 118:334–345. https://doi.org/10.1111/j.1600-0706.2008.17116.x
96. Raven PH, Gereau RE, Phillipson PB, Chatelain C, Jenkins CN, Ulloa U, C (2020) The distribution of biodiversity richness in the tropics. Sci Adv 6:eabc6228. https://doi.org/10.1126/sciadv.abc6228
97. Reimuth J, Zotz G (2020) The biogeography of the megadiverse genus *Anthurium* (Araceae). Bot J Linn Soc 194:164–176. https://doi.org/10.1093/botlinnean/boaa044
98. Ribeiro BR, Velazco SJE, Guidoni-Martins K, Tessarolo G, Jardim L, Bachman SP, Loyola R (2022) bdc: A toolkit for standardising, integrating and cleaning biodiversity data. Methods Ecol Evol 13:1421–1428. https://doi.org/10.1111/2041-210X.13868
99. Richardson BA, Rogers C, Richardson MJ (2000) Nutrients, diversity, and community structure of two phytotelm systems in a lower montane forest, Puerto Rico: Nutrients and phytotelm community structure. Ecol Entomol 25:348–356. https://doi.org/10.1046/j.1365-2311.2000.00255.x

100. Rivers MC, Taylor L, Brummitt NA, Meagher TR, Roberts DL, Nic Lughadha E (2011) How many herbarium specimens are needed to detect threatened species? Biol Conserv 144:2541–2547. https://doi.org/10.1016/j.biocon.2011.07.014
101. Rondinini C, Di Marco M, Visconti P, Butchart SH, Boitani L (2014) Update or outdate: long-term viability of the IUCN Red List. Conserv Lett 7:126–130. https://doi.org/10.1111/conl.12040
102. Sala OE, Chapin FS, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A, Leemans R, Lodge DM, Mooney HA, Oesterheld M, Poff NLR, Sykes MT, Walker BH, Walker M, Wall DH (2000) Global biodiversity scenarios for the year 2100. Science 287:1770–1774. https://doi.org/10.1126/science.287.5459.1770
103. Schoener TW, Spiller DA (1987) High population persistence in a system with high turnover. Nature 330:474–477. https://doi.org/10.1038/330474a0
104. Smith AR (1972) Comparison of fern and flowering plant distributions with some evolutionary interpretations for ferns. Biotropica 4:4–9. https://doi.org/10.2307/2989639
105. Sodhi NS, Koh LP, Peh KS-H, Tan HTW, Chazdon RL, Corlett RT, Lee TM, Colwell RK, Brook BW, Sekercioglu CH, Bradshaw CJA (2008) Correlates of extinction proneness in tropical angiosperms: Extinction proneness in tropical angiosperms. Divers Distrib 14:1–10. https://doi.org/10.1111/j.1472-4642.2007.00398.x
106. Solano R, Cruz G, Martínez A, Lagunez L (2010) Plantas utilizadas en la celebración de la Semana Santa en Zaachila, Oaxaca, México. Polibotánica 29
107. Soria-Auza RW, Kessler M (2008) The influence of sampling intensity on the perception of the spatial distribution of tropical diversity and endemism: a case study of ferns from Bolivia: Influence of sampling intensity on patterns of tropical diversity. Divers Distrib 14:123–130. https://doi.org/10.1111/j.1472-4642.2007.00433.x
108. Stevens GC (1989) The latitudinal gradient in geographical range: how so many species coexist in the tropics. Am Nat 133:240–256
109. Stuntz S, Ziegler C, Simon U, Zotz G (2002) Diversity and structure of the arthropod fauna within three canopy epiphyte species in central Panama. J Trop Ecol 18:161–176. https://doi.org/10.1017/S0266467402002110
110. Subedi A, Kunwar B, Choi Y, Dai Y, van Andel T, Chaudhary RP, de Boer HJ, Gravendeel B (2013) Collection and trade of wild-harvested orchids in Nepal. J Ethnobiol Ethnomed 9:64. https://doi.org/10.1186/1746-4269-9-64
111. Tabarelli M, Pinto LP, Silva JMC, Hirota M, Bede L (2005) Challenges and opportunities for biodiversity conservation in the Brazilian Atlantic Forest. Conserv Biol 19:695–700. https://doi.org/10.1111/j.1523-1739.2005.00694.x
112. Taylor A, Zotz G, Weigelt P, Cai L, Karger DN, König C, Kreft H (2021) Vascular epiphytes contribute disproportionately to global centers of plant diversity. Glob Ecol Biogeogr 31:62–74. https://doi.org/10.1111/geb.13411

113. Ticktin T, Mondragón D, Lopez-Toledo L, Dutra-Elliott D, Aguirre-León E, Hernández-Apolinar M (2020) Synthesis of wild orchid trade and demography provides new insight on conservation strategies. Conserv Lett 13:e12697. https://doi.org/10.1111/conl.12697

114. Thomas BA (2006) Slippers, thieves and smugglers — Dealing with the illegal international trade in orchids. Environ Law Rev 8:85–92. https://doi.org/10.1350/enlr.2006.8.2.85

115. Thomsen MS, Altieri AH, Angelini C, Bishop MJ, Gribben PE, Lear G, He Q, Schiel DR, Silliman BR, South PM, Watson DM, Wernberg T, Zotz G (2018) Secondary foundation species enhance biodiversity. Nat Ecol Evol 2:634–639. https://doi.org/10.1038/s41559-018-0487-5

116. UNEP-WCMC (2022) Protected areas map of the world, March 2022. (accessed 3.11.22)

117. Vergara-Rodríguez D, Mathieu G, Samain MS, Armenta-Montero S, Krömer T (2017) Diversity, distribution, and conservation status of *Peperomia* (Piperaceae) in the state of Veracruz, Mexico. Trop Conserv Sci 10:1–28. https://doi.org/10.1177/1940082917702383

118. Werner FA, Köster N, Kessler M, Gradstein SR (2011) Is the resilience of epiphyte assemblage to human disturbance a function of local climate? https://doi.org/10.5167/UZH-76892

119. Williams SE, Williams YM, VanDerWal J, Isaac JL, Shoo LP, Johnson CN (2009) Ecological specialisation and population size in a biodiversity hotspot: How rare species avoid extinction. Proceedings of the National Academy of Sciences 106, 19737–19741. https://doi.org/10.1073/pnas.0901640106

120. Zizka A (2019) Big data suggest migration and bioregion connectivity as crucial for the evolution of Neotropical biodiversity. Front Biogeogr 11. https://doi.org/10.21425/F5FBG40617

121. Zizka A, Antunes Carvalho F, Calvente A, Rocio Baez-Lizarazo M, Cabral A, Coelho JFR, Colli-Silva M, Fantinati MR, Fernandes MF, Ferreira-Araújo T, Lambert Moreira G, Santos F, Santos NMC, dos Santos-Costa TAB, Serrano RC, Alves FC, da Silva AP, de Souza Soares A, de Cavalcante PG, Tomaz C, Vale E, Vieira VF, Antonelli TL, A (2020a) No one-size-fits-all solution to clean GBIF. PeerJ 8:e9916. https://doi.org/10.7717/peerj.9916

122. Zizka A, Azevedo J, Leme E, Neves B, da Costa AF, Caceres D, Zizka G (2020b) Biogeography and conservation status of the pineapple family (Bromeliaceae). Divers Distrib 26:183–195. https://doi.org/10.1111/ddi.13004

123. Zizka A, Silvestro D, Andermann T, Azevedo J, Duarte Ritter C, Edler D, Farooq H, Herdean A, Ariza M, Scharn R, Svantesson S, Wengström N, Zizka V, Antonelli A (2018) CoordinateCleaner: Standardised cleaning of occurrence records from biological collection databases. Methods Ecol Evol 10:744–751. https://doi.org/10.1111/2041-210X.13152

124. Zizka A, Silvestro D, Vitt P, Knight TM (2021) Automated conservation assessment of the orchid family with deep learning. Conserv Biol 35:897–908. https://doi.org/10.1111/cobi.13616

125. Zotz G (2016) Plants on plants – the biology of vascular epiphytes, Fascinating Life Sciences. Springer, Switzerland

126. Zotz G (2013) Hemiepiphyte': a confusing term and its history. Ann Botany 111:1015–1020

127. Zotz G, Bader MY (2009) Epiphytic plants in a changing world-global: change effects on vascular and non-vascular epiphytes. Progress in Botany 70:147–170. https://doi.org/10.1007/978-3-540-68421-3_7

128. Zotz G, Bogusch W, Hietz P, Ketteler N (2010) Growth of epiphytic bromeliads in a changing world: The effects of CO2, water and nutrient supply. Acta Oecol 36:659–665. https://doi.org/10.1016/j.actao.2010.10.003

129. Zotz G, Almeda F, Bautista-Bello AP, Eskov A, Giraldo-Cañas D, Hammel B, Harrison R, Köster N, Krömer T, Lowry PP, Moran RC, Plunkett GM, Weichgrebe L 2021a. Hemiepiphytes revisited. Perspectives in Plant Ecology,Evolution and Systematics51,125620. https://doi.org/10.1016/j.ppees.2021.125620

130. Zotz G, Weigelt P, Kessler M, Kreft H, Taylor A (2021b) EpiList 1.0: a global checklist of vascular epiphytes. Ecology 102:e03326. https://doi.org/10.1002/ecy.3326

131. Zuleta D, Benavides AM, López-Rios V, Duque A (2016) Local and regional determinants of vascular epiphyte mortality in the Andean mountains of Colombia. J Ecol 104:841–849

Figures

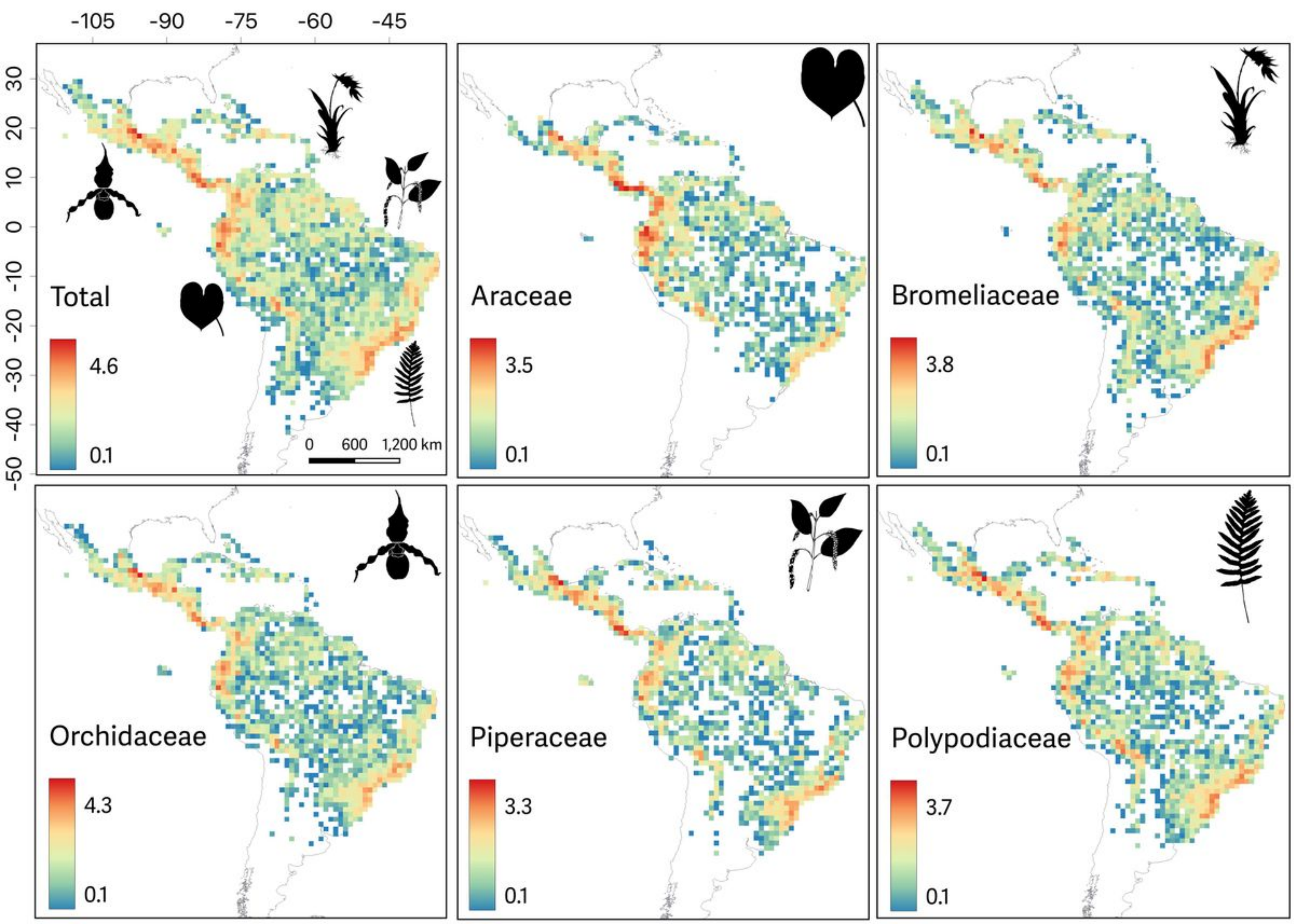

Figure 1

The number of occurrence records (log-transformed) of the richest vascular epiphyte families per 1-degree grid-cell within the Neotropical region. Representative silhouettes of taxa used in figures 1 and 2 were taken from PhyloPic version 2.0. under Attribution-NonCommercial-ShareAlike 3.0 Unported (https://creativecommons.org/licenses/by-nc-sa/3.0/). For Araceae (German R. Verdilak, https://www.phylopic.org/images/7dc1b40b-c27a-4a2a-b8f1-d78ac92bbb90/anthurium-clarinervium), Bromeliaceae (Maija Karala; https://www.phylopic.org/images/e16c940c-f73d-43a2-824b-f3582012a93e/tillandsia-dyeriana), Orchidaceae (Mason McNair, https://www.phylopic.org/images/bb459b30-2370-4b7f-a1f9-f0d836aa35d1/cypripedium-kentuckiense), Piperaceae (Melissa Ingala, https://www.phylopic.org/images/45553c37-70c3-4261-a9ee-d7f525529c90/piper), and Polypodiaceae (Mason McNair, https://www.phylopic.org/images/aea1dbe9-4d59-4d3f-992e-994fc4c10365/polypodium-glycyrrhiza).

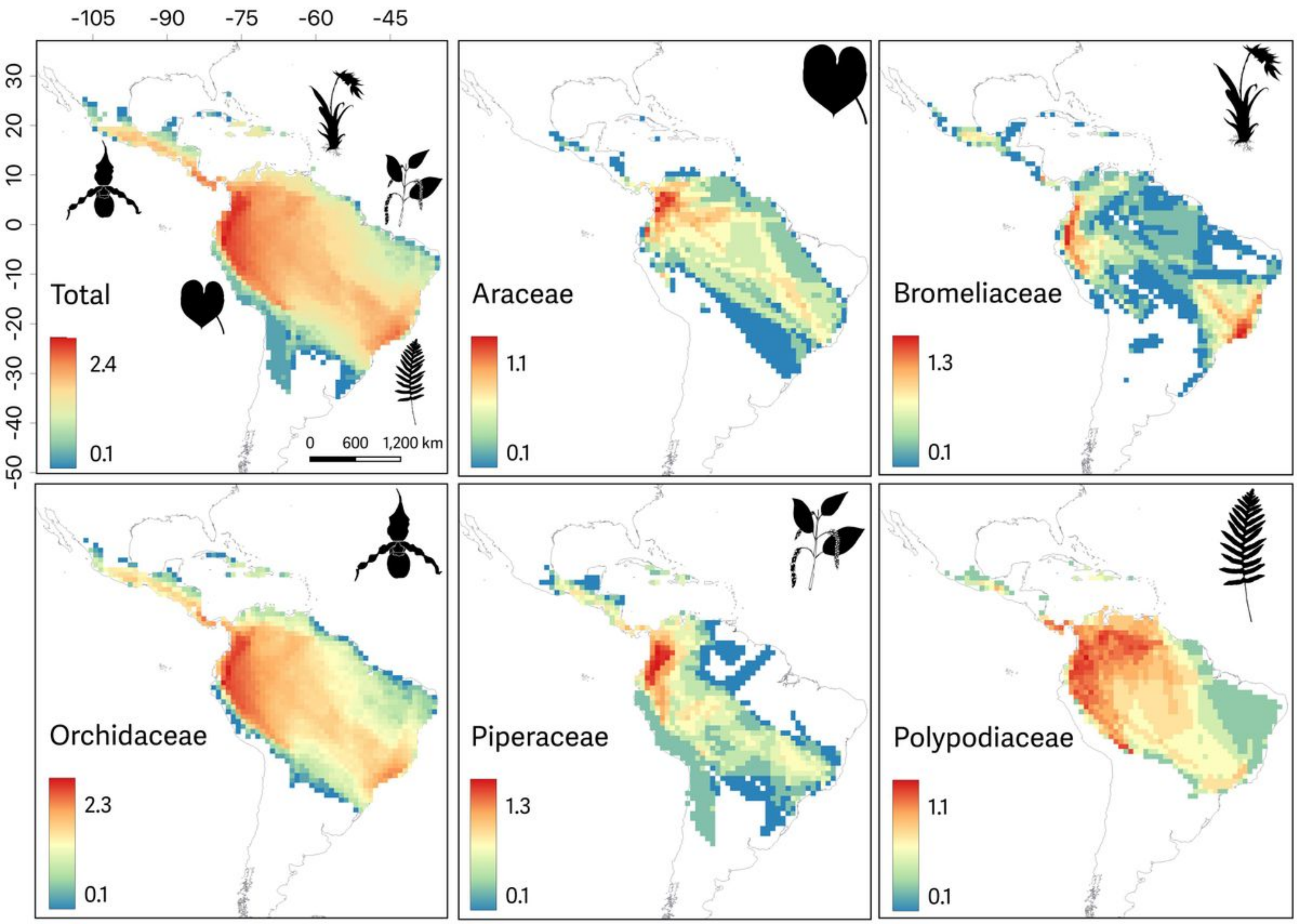

Figure 2

The number of threatened epiphyte species (log-transformed) at a 1-degree resolution within the Neotropics.

Supplementary Files

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