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Endemism Centres of the Five Richest Vascular Epiphyte Families in the Neotropics

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ABSTRACT

Aim: Endemic species, characterised by limited geographic ranges, face a high risk of extinction. The neotropical region harbours diverse ecosystems and a substantial number of endemic species, thus identifying areas of high endemism is crucial for protecting unique and threatened species and ecosystems. Vascular epiphytes—nonparasitic plants that grow on other plants without contact with the soil—exhibit remarkable diversity in the neotropics, with 63% of the global total of ca. 31,000 epiphyte species found in this region. This study aims to describe the endemism centres for the five most species-rich families of vascular epiphytes.

Location: Neotropics.

Taxon: Tracheophyta.

Methods: We gathered information from free-access web repositories, specific epiphytic plant databases and scientific and grey literature on epiphyte species of the families Araceae, Bromeliaceae, Orchidaceae, Piperaceae and Polypodiaceae within the neotropical realm as defined by Morrone et al. (2022). Geographical ranges were calculated using minimum convex polygons for 11,446 species, accounting for about 70% of all epiphyte species in the neotropics. Narrow endemic species were defined as those within the first quartile of the density distribution of geographic range sizes within each family and we identified endemism centres for epiphyte species of the five families.

Results: Our study identified endemism centres for vascular epiphyte species in several biogeographic provinces, including Paramo, Cauca, Guatuso-Talamanca, Atlantic, Yungas and Puntarenas-Chiriqui. Orchidaceae, accounting for most of the analysed species (71%), drove the overall distribution pattern; however, endemism patterns varied among families.

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Main Conclusions: Regions with high epiphyte richness exhibited a greater proportion of endemic species, though the composition of epiphyte species varied considerably among regions. The endemism centres identified in this study could be prioritised as conserved and protected areas.

1 | Introduction

Endemism is a fundamental concept in biogeography that refers to the exclusive occurrence of taxa within a particular geographic region or ecosystem (Gaston 1994). Endemic species are often found in isolated habitats that offer unique ecological and evolutionary conditions, facilitating speciation and adaptation. The presence of endemism serves as a crucial indicator of a region's environmental uniqueness and evolutionary history and endemic or rare species play a vital role in sustaining overall diversity (Mittermeier et al. 2011). Because endemic species are often adapted to specific local conditions, they may be particularly vulnerable to environmental changes and anthropogenic disturbances, such as habitat destruction, climate change or the introduction of nonnative species (Mittermeier et al. 2011). The loss of endemic species can have ecological and evolutionary impacts, including changes in community structure and function and the decline of genetic diversity (Gaston 1994).

Identifying areas with high levels of endemism is crucial for effective conservation strategies targeting unique and threatened species and ecosystems (Mittermeier et al. 2011). However, quantifying endemism presents challenges, especially in regions where there are large knowledge gaps or insufficient data on other biodiversity indicators. Additionally, the quantification of endemism is influenced by several factors, such as the biogeography of the area, environmental conditions and the historical and inherent characteristics of the taxon, making it difficult to establish a generally applicable definition (Médail and Baumel 2018). So far, various methods have been developed to define endemism, including approaches based on range size, taxonomic distinctness and phylogenetic data (Laffan and Crisp 2003; Rosauer et al. 2009). Endemism, as a concept, is inherently dependent on scale (Daru et al. 2020), but the definition of range restrictedness is widely used in the literature, also called microendemism, narrow endemism, local endemism, range-restricted endemism or short-range endemism (e.g., Caesar, Grandcolas, and Pellens 2017; Médail and Baumel 2018). Narrow endemic species, hereafter endemics, are defined as the most narrowly distributed species, for example, those in the first quartile of the density distribution of the geographic range sizes within a given taxon (Gaston 1994).

The neotropical realm, which encompasses tropical America, harbours one of the largest assemblages of endemic plant and animal species, making it one of the most biodiverse regions in the world (Burbano-Girón et al. 2022). Particularly noteworthy areas within this realm include the Andes (Gentry and Dodson 1987), the Atlantic Forest (Freitas et al. 2016), Mesoamerica (Megamexico; Rivera-Martínez et al. 2022) and the Guiana Shield (Givnish et al. 2007), all characterised by a high concentration of endemic species. This concentration of endemic taxa can be attributed to geological and climatic changes that have given rise to diverse habitats and microclimates

(Antonelli et al. 2018). These environmental conditions fostered isolated diversification and evolution (Ricklefs 2007). Events such as the Andean uplift, the closing of the Isthmus of Panama and the persistence of the Guiana Shield, along with the region's diverse biota, have driven unique adaptations and numerous endemic species (Antonelli et al. 2018).

The neotropics is also the most diverse biogeographical realm in terms of vascular epiphytes (Taylor et al. 2021), that is, plants that live nonparasitically on other plants for their entire life without connection to the soil (Zotz 2016). Epiphytes with ca. 31,000 species represent a substantial part of global vascular plant richness (ca. 10%; Zotz et al. 2021), and fulfil many ecosystem services by influencing water economy, buffering temperature fluctuations or reducing daytime vapour pressure deficit (Gotsch, Nadkarni, and Amici 2016). Furthermore, epiphytes provide resources to other taxonomic groups (e.g., food and habitat for birds, bats, frogs and arthropods). These services are particularly pronounced in areas where they are species-rich and abundant, such as the neotropics.

Among the most representative and diverse families of vascular epiphytes in the neotropics are Araceae, Bromeliaceae, Orchidaceae, Piperaceae and Polypodiaceae (Taylor et al. 2021; Zotz et al. 2021). These five families, together with Ericaceae, account for 90% of total epiphyte richness in the neotropics (ca. 17,430; Taylor et al. 2021). At the continental scale, richness and endemism patterns for families or groups that include many epiphyte species have been studied for, for example, Bromeliaceae (Zizka et al. 2020), Cactaceae (Barthlott et al. 2015), ferns (Suissa, Sundue, and Testo 2021) and the megadiverse genus *Anthurium* in the Araceae (Reimuth and Zotz 2020). However, there are no studies on endemism for vascular epiphytes at continental scales, such as the neotropics, considering the most representative taxa of this group (but see Morawetz and Raedig 2007 for angiosperms).

Therefore, using a newly compiled set of geographic data, this study aimed to identify endemism centres in the neotropics of the five richest epiphyte families Araceae, Bromeliaceae, Orchidaceae, Piperaceae and Polypodiaceae.

We hypothesise and predict that: (1) distinct endemism centres exist within the neotropics for these epiphytic families, reflecting the region's diverse habitats and climatic conditions (Ricklefs 2007). Based on the literature, we specifically predicted that Araceae will be highly endemic in the Andes (Croat and Ortiz 2020), Bromeliaceae in the Atlantic Forest, the central Andes, southern Venezuela and southern Mexico (Zizka et al. 2020), Orchidaceae in the Ecuadorian and Bolivian Andes (Figure 3 in Vitt et al. 2023), while for Piperaceae and Polypodiaceae, no specific predictions can be made, but endemism is most likely prevalent in mountainous areas. (2) areas with high levels of endemism of epiphytes also exhibit

significant overlap with other biodiversity hotspots (Mittermeier et al. 2011), which underscores their conservation importance. A congruence between richness and endemism is observed in coarser and larger scales for terrestrial vegetation and other taxa e.g., (Prado et al. 2015) and is expected to apply for epiphytes as well.

2 | Methods

2.1 | Study Area

We focus on the neotropics following Morrone et al. (2022), who defined the neotropical realm as the tropical areas of America, including three subregions (Antillean, Brazilian and Chacoan) and two transition zones (Mexican and South American), and explicitly excluded 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 and northern Mexico were also excluded as they belong to the Nearctic region (Holarctic realm; Morrone 2014).

As the distribution of species rarely coincides with political units (Olson et al. 2001), we performed the analysis within the context of biologically defined units, namely, biogeographic provinces (Morrone et al. 2022). This approach is better suited to identify areas of outstanding biodiversity and representative communities since it emphasises the importance of endemic genera and families (higher taxa), distinct assemblages of species and the imprint of geological history on the distribution of plants and animals (Olson et al. 2001). This classification includes 57 biogeographic provinces (province names are presented in Appendix S3).

2.2 | Database

We compiled a database of geo-referenced records of species of the five most species-rich families of vascular epiphytes (from now on epiphytes): Araceae, Bromeliaceae, Orchidaceae, Piperaceae, and Polypodiaceae. We gathered information from free-access web repositories (e.g., GBIF), specific epiphytic plant databases (e.g., EpiG-DB v1 database; Mendieta-Leiva et al. 2020) and scientific and grey literature (see Carmona-Higuaita et al. 2024). Data sources can be reviewed in Appendix S3. To ensure accuracy, we addressed geographic and taxonomic errors in our dataset (for the detailed process, see Carmona-Higuaita et al. 2024). We focused exclusively on holo- and hemiepiphytes, that is, species that grow epiphytically for their entire life and hemiepiphyte species that initially grow as true epiphytes but establish root contact with the soil later respectively (for terminology, see Zotz 2021). Nomadic vines, which are climbing plants that do not have an epiphytic phase as they maintain contact with the soil, were excluded from our analysis. We utilised a modified version of EpiList 1.0 (Carmona-Higuaita et al. 2024; Zotz et al. 2021) for this purpose (see fully modified EpiList in Appendix S4). Lastly, we eliminated any duplicated records to ensure data integrity.

Evaluating the effect of sampling effort on observed patterns is a fundamental problem of any biogeographic study (Gaston 1994; Magurran 2004). To overcome these limitations,

we used the KnowB function of the R package ‘KnownBR’ (Lobo et al. 2018) to identify areas with the highest and lowest knowledge of epiphytes richness. This approach estimates species accumulation curves for each geographic unit under examination and estimates the survey completeness intrinsic to the database. We estimated survey completeness by adjusting the species accumulation curve to the Michaelis–Menten equation (Clench 1979) and using the exact method within grid cells of 1° (~110 × 100 km). The final slope of the accumulation curve gives the amount of effort necessary to complete the survey within a particular geographic unit (Lobo et al. 2018). The values of slope and completeness indicate the quality of the survey conducted in each geographic unit. Lower values of slope and greater values of completeness define the best-surveyed areas. We removed poorly sampled grid cells containing less than 10 records. All analyses were performed using the software R version 4.2.2 (R Core Team 2022).

2.3 | Species Richness and Endemism

Richness estimation based on distribution maps may give a better estimate of species richness at large geographic scales than occurrence records whenever data are sparse (raw data; Töpel et al. 2016). Thus, our species richness and endemism maps were built by stacking the species ranges with the biogeographic provinces. To approximate species ranges from occurrence data (i.e., extents of occurrence; Gaston 1994), we generated a minimum pseudo-spherical convex hull using the function CalcRange of the ‘speciesgeocodeR v. 2.0-10’ package (Töpel et al. 2016). We excluded species with invalid polygons, that is, those in which segments intersected did not have three vertices (including species with one or two records), but those were added later to the list of species as narrow endemics. All geographic ranges of species were intersected with land masses, that is, the polygons were cut to limit their extent to that of the neotropics to exclude marine areas.

We applied the quartile definition to determine a species as a narrow endemic, that is, a taxon whose geographical range is distributed within the first quartile of the geographic range size of all species in its family (Gaston 1994). Endemism was evaluated separately for each family since epiphytism developed within different phylogenetic lineages (epiphytes are a polyphyletic group; Zotz 2016), so separate taxonomic analyses can show how these phylogenetic origins result in distinctive biogeographical patterns (Willinghöfer, Cicuzza, and Kessler 2012). The number of endemic species was counted for each biogeographic unit (i.e., province). Finally, we used Quantum GIS v. 3.22 to present our results (QGIS.org 2022).

3 | Results

We obtained 1,892,483 occurrence records of epiphytes within the neotropics. After geographic cleaning and taxonomic scrubbing, we retained 581,848 records of 11,446 species, 8097 epiphyte species of Orchidaceae (71% of all species in the dataset), 1617 (14%) of Bromeliaceae, 675 (6%) of Araceae, 606 (5%) of Polypodiaceae and 451 (4%) of Piperaceae (see complete species list in Appendix S4). GBIF contributed most of the data (41%),

followed by the EpIG database (23%). Twelve other sources accounted for the remaining 36% of the records (Carmona-Higuita et al. 2024; Appendix S3). The analysed species were widely distributed throughout the neotropics, from northern Mexico to southern Brazil and northern Argentina (Figure 1). We identified well-known areas with high species richness, which included Mexico, Central America, Ecuador, the Andes and the eastern coast of Brazil (Figure 2). We found that the regions with higher species numbers matched the areas with higher number of records.

In the neotropics, regions with high species richness of epiphytes include the Andes, particularly in the Paramo and Cauca

provinces, accounting for 11.4% of the total species. Additionally, the Napo and Magdalena provinces contribute 7.1% to the overall species count. Central America exhibits significant richness in the Guatuso-Talamanca and Puntarenas-Chiriquí provinces, representing 7.1% of the total. Along the eastern coast of Brazil, the Rondonia and Atlantic provinces show a substantial presence with 6.6% of the species. In contrast, lower species numbers are observed in various regions of South America, such as Chaco (1.9%), Xingu-Tapajos and Caatinga provinces (1.8%). Additionally, relatively arid regions like the Trans-Mexican Volcanic Belt (1.9%) and Yucatan peninsula provinces (1.6%) in Mexico, as well as the Guajira province (1.4%) in Colombia, display comparatively lower levels of species richness (Figure 3).

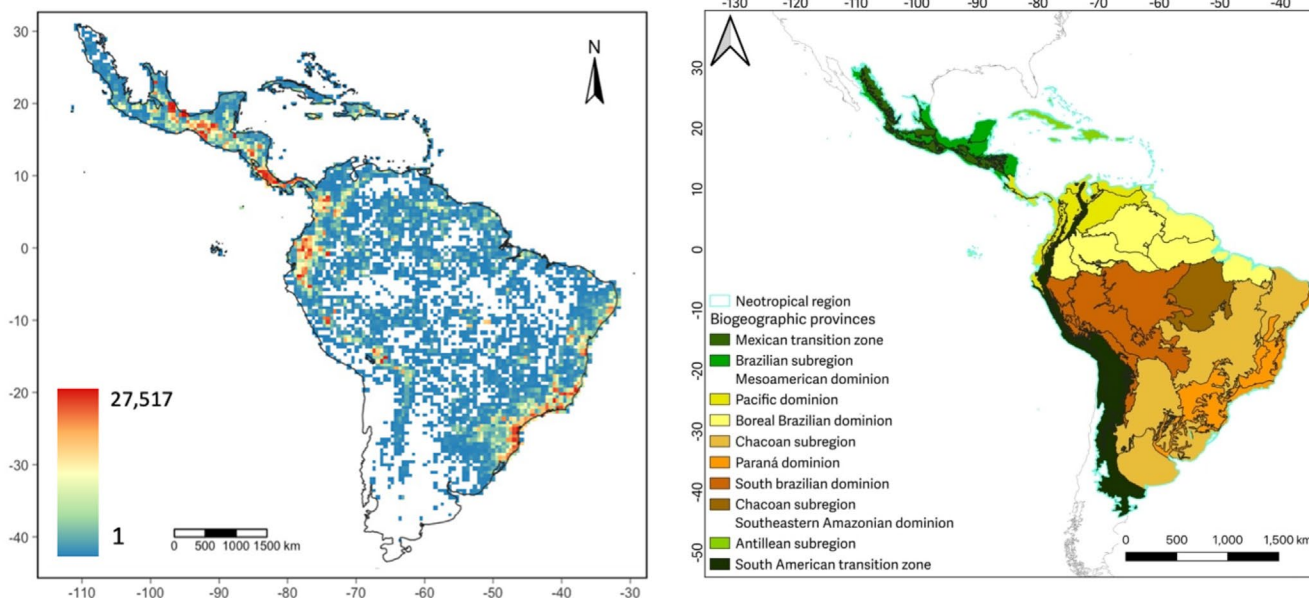


FIGURE 1 | Number of records per 0.5° grid cell for the five richest vascular epiphyte families within the neotropical region (left) and biogeographic provinces within the neotropics coloured by dominion (right).

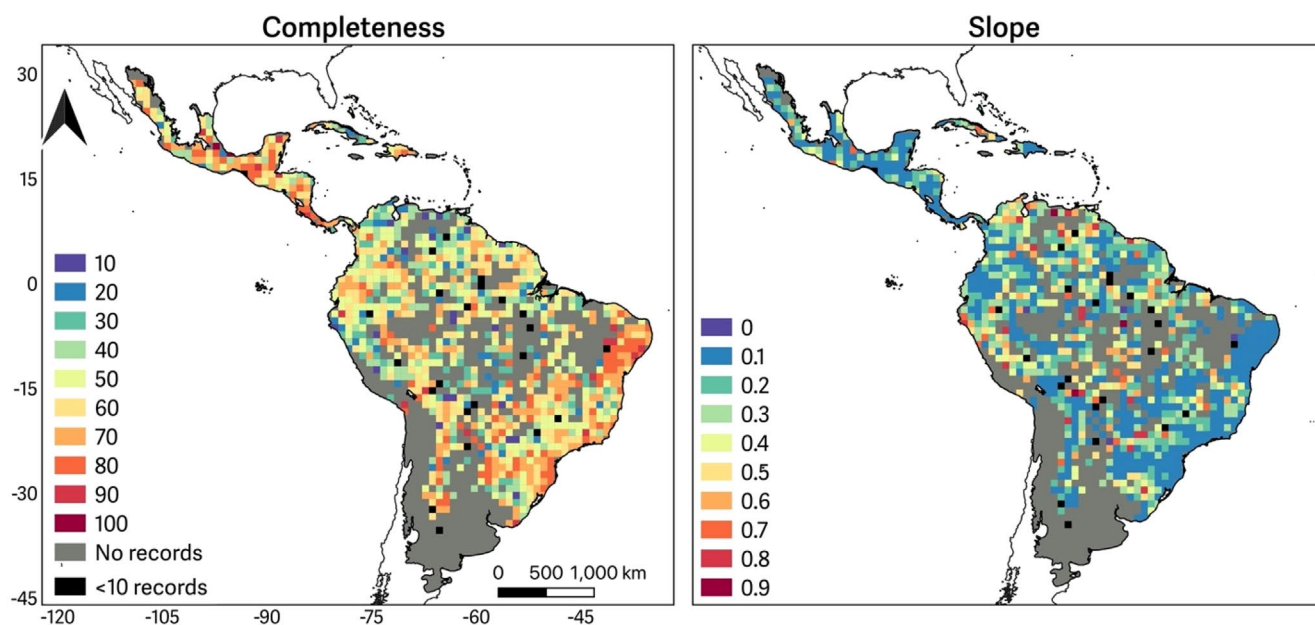


FIGURE 2 | Survey completeness and slope of the accumulation curve for all vascular epiphyte species combined in the neotropical region. Lower values of slope and greater values of completeness define the best-surveyed areas.

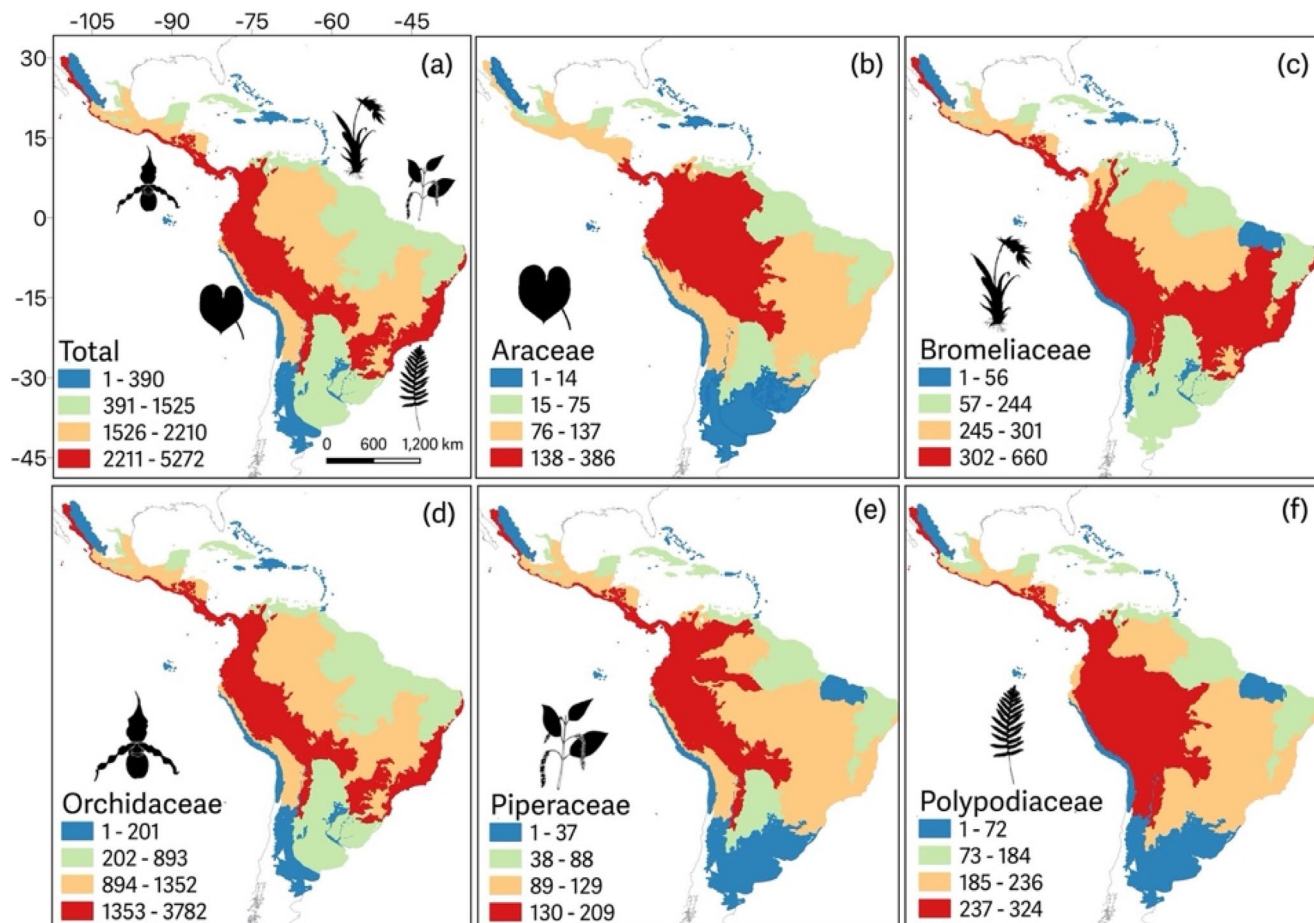


FIGURE 3 | Richness per biogeographic provinces of all vascular epiphyte species combined (total) and the five richest families in the neotropics individually, based on convex polygons.

The richness of epiphytic plant families varies across different biogeographic provinces in the neotropics. Araceae shows the highest richness in the Paramo (7.0%), Cauca (6.4%) and Chocó-Darién (4.9%) provinces in the Andean region and Northern South America. Bromeliaceae exhibits a high number of species in the Atlantic (5.5%) and Parana Forest (4.4%) provinces in Brazil, as well as in the Paramo province (4.8%). Orchidaceae drives the general distribution pattern, accounting for 71% of the analysed species. Its highest richness is mainly in the northern Andes, particularly in the Paramo (7.4%) and Cauca (5.6%) provinces, as well as in the Guatuso-Talamanca province (3.9%) of Central America and the inter-Andean valleys of the Magdalena province (3.9%). Piperaceae shows high richness in the Paramo (4.3%) and Cauca (3.7%) provinces in the Northern Andes, the Rondonia province (3.5%) in Brazil and the Napo province (3.3%) in Ecuador and Peru. Polypodiaceae exhibits its greatest richness in the Paramo (3.5%) and Cauca (3.1%) provinces in the Northern Andes, the Yungas (3.3%) and Rondonia (3.1%) provinces in Argentina and the Guatuso-Talamanca (3.1%) and Puntarenas-Chiriquí (3.0%) provinces in Central America (Table 1 and Appendix S3).

The number of species records varied across individual species, with *Anthurium scandens* (4425 records) and *Tillandsia recurvata* (3355 records) having the largest number of available

records. An additional 57 species had more than 1000 records, although the median number of records per species was only six (mean = 51, SD = 154). However, for 3347 species (29%), there were fewer than three records in the database, making it impossible to calculate their geographic range. The geographic range sizes varied from 1 to 17,371,300 km². *Tillandsia recurvata* exhibited the broadest distribution (median = 9962 km², mean = 1,123,848 km², SD = 2,730,094 km²; see density curves in Appendix S2), covering approximately 95% of the neotropics' area. Additionally, six other species occupied around 95% of the neotropics, namely, *Pleopeltis polypodioides*, *P. macrocarpa* and *Phlebodium aureum* (Polypodiaceae), *Peperomia tetraphylla* (Piperaceae), *Tillandsia usneoides* (Bromeliaceae) and *Isochilus linearis* (Orchidaceae). Among all species, 2853 (21%) were found to be endemic as defined here, that is, with the narrowest distribution within each family's first quartile of the density distribution of geographic range sizes (Gaston 1994; see Appendix S4). Orchids constituted most of them (2287 spp., 83% of total endemic species), driving the general pattern of endemism centres, followed by bromeliads with 284 spp. (=10%). Notably, 40% of the endemic species belonged to just ten genera, that is, *Anthurium* (Araceae) with 71 species, *Tillandsia* (Bromeliaceae) with 72 species and *Stelis*, *Lepanthes*, *Epidendrum*, *Masdevallia*, *Pleurothallis*, *Telipogon* and *Acianthera* (all Orchidaceae) together with 827 species.

TABLE 1 | Richness of vascular epiphyte species in the neotropics, including total and individual counts for the five richest families, across the 10 richest biogeographic provinces.

Province	Total	Araceae	Bromeliaceae	Orchidaceae	Piperaceae	Polypodiaceae
Paramo province	5272	386	571	3782	209	324
Cauca province	4124	352	428	2876	183	285
Guatuso-Talamanca province	3045	250	344	2014	154	283
Napo province	2954	246	400	1883	162	263
Magdalena province	2897	227	301	1944	154	271
Puntarenas-Chiriqui province	2863	220	329	1898	141	275
Yungas province	2801	137	366	1834	160	304
Rondonia province	2633	150	359	1667	172	285
Atlantic province	2568	118	660	1481	101	208
Ucayali province	2530	188	359	1595	134	254

TABLE 2 | Number of endemic species per biogeographic provinces of all vascular epiphyte species combined (total) and the five richest families in the neotropics individually.

Province	Total	Araceae	Bromeliaceae	Orchidaceae	Piperaceae	Polypodiaceae
Paramo province	800	32	33	708	16	11
Cauca province	501	25	14	451	7	4
Guatuso-Talamanca province	321	30	18	264	5	4
Atlantic province	272	3	86	175	2	6
Yungas province	262	1	10	232	11	8
Puntarenas-Chiriqui province	231	13	13	202	2	1
Magdalena province	202	5	3	188	4	2
Rondonia province	102	0	5	78	15	4
Parana Forest province	93	1	25	63	2	2
Choco-Darien province	83	25	2	56	0	0

For all epiphytes combined, the richest provinces showed the highest concentration of endemic species. The Paramo province stood out with 20.6% of the total epiphytes analysed, followed by Cauca (12.9%), Guatuso-Talamanca (8.3%), Atlantic (7.0%), Yungas (6.7%) and Puntarenas-Chiriqui (5.9%). In contrast, the provinces with the lowest numbers of endemic species were the Yucatan Peninsula, Cayman Islands, Esteros del Ibera and Atacama, each accounting for less than 0.1% (Table 2).

Among the families, Araceae had the highest numbers of endemic species, primarily in the Paramo (20.1%), Guatuso-Talamanca (18.9%), Cauca (15.7%) and Chocó-Darién (15.7%) provinces. Bromeliaceae showed a high number of endemic species in the Atlantic (23.2%), Paramo (8.9%) and Parana Forest (2.4%) provinces. Orchidaceae displayed its highest endemism concentration in the Paramo (22.5%), Cauca (12.9%), Guatuso-Talamanca (8.4%) and Yungas (7.4%) provinces. For Piperaceae, a high number of endemics were observed in the Paramo (14.2%), Rondonia (13.3%), Yungas (9.7%) and Cauca

(6.2%) provinces. Polypodiaceae exhibited the highest numbers of endemic species in the Paramo (12.1%), Guianan (9.9%), Yungas (8.8%), Atlantic (6.6%) and Rondonia (4.4%) provinces (Figure 4, Appendix S3).

4 | Discussion

4.1 | Insights of the Data Review

The compiled database encompasses nearly two million records covering 11,446 species of epiphytes in the neotropics, accounting for 66% of the region's known species total (Taylor et al. 2021). Despite extensive coverage, certain provinces within the neotropics, such as Amazonia, a few relatively dry areas, and the southern provinces of Argentina and Chile, have a limited number of records and species (Figure 1), which could be the result of a sampling bias or unfavourable environmental conditions (Nelson et al. 1990). Previous studies have highlighted the under-sampling and biased representation of

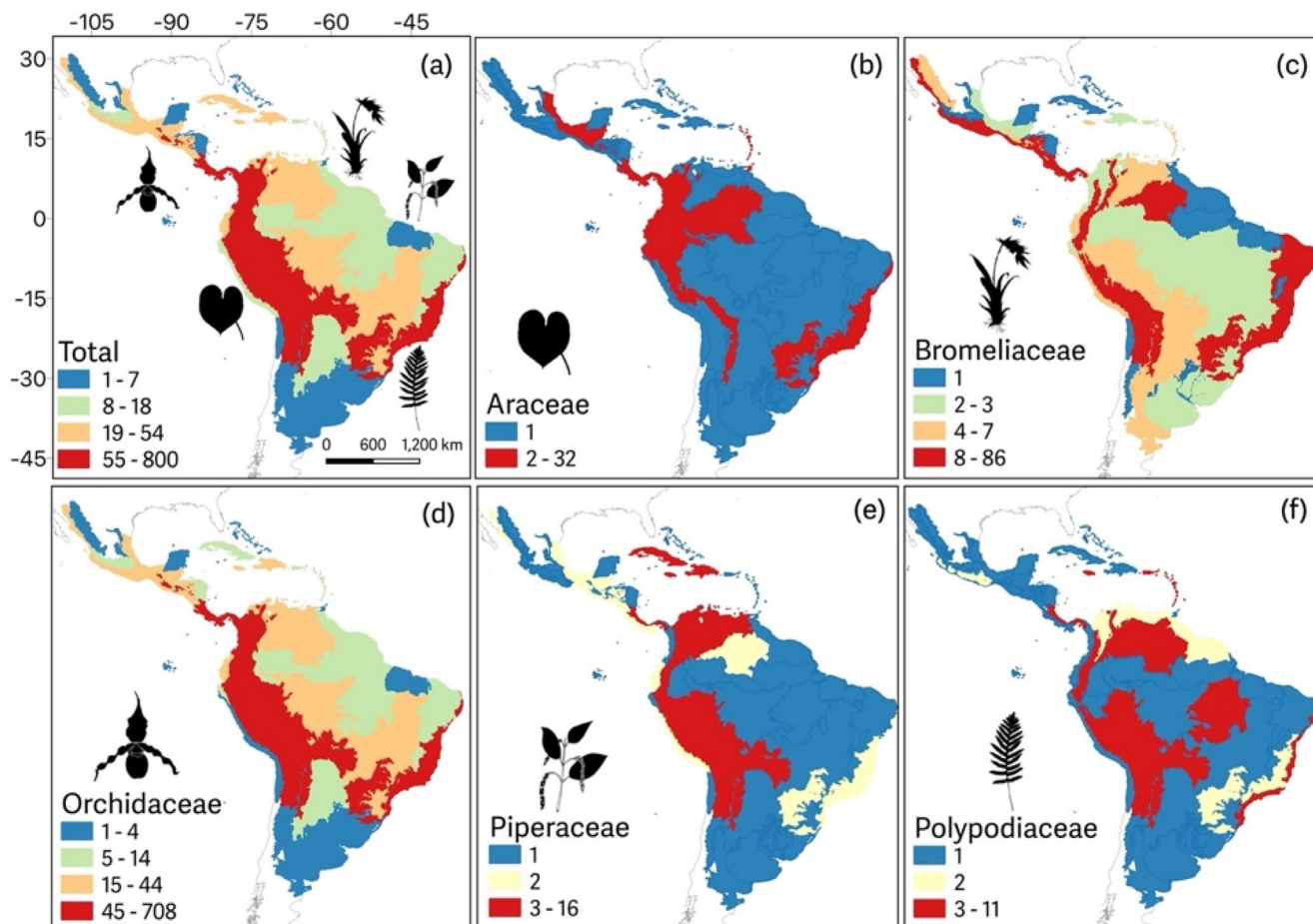


FIGURE 4 | The number of endemics per biogeographic provinces of all vascular epiphyte species combined (total) and the five richest families in the neotropics individually based on convex polygons.

epiphytes in the Atlantic Forest and Amazonia, influenced by factors such as accessibility, biological attractiveness and land use (Araujo, Quaresma, and Ramos 2022; Araujo and Ramos 2021). However, we identified well-sampled areas with high species richness, which include Mexico, Central America, Ecuador, the Andes and the eastern coast of Brazil (Figure 2, see Appendix S1).

The compiled database combines both published and unpublished data from many sources. However, it still remains incomplete due to the limited digitisation of data stored in herbaria, particularly from smaller, local herbaria in Latin American countries (Delves et al. 2024). Nonetheless, the utilisation of global and national databases can help mitigate inventory gaps, as evidenced by a study on epiphyte sampling in Amazonia (Araujo, Quaresma, and Ramos 2022). While acknowledging potential errors in our range maps, such as misplaced records or misidentification of species, these discrepancies are not expected to introduce a systematic bias into the overall pattern of epiphyte distributions for each studied family due to the robust representativeness of our data. The consideration of large species assemblages concurrently enables the identification of strong macroecological relationships emerging from species-specific patterns (Kerr, Kharouba, and Currie 2007).

4.2 | Endemism Centres

The proportion of narrow endemic species was 21% of the total, which fell below the expected 25% (i.e., quartile definition) due to approximately 446 species with invalid polygons, which were excluded from the endemism threshold quantification. To contextualise our findings, it is worth noting that the distribution ranges of around 60% of the analysed species fell under the threshold employed by the IUCN Red List to classify species as 'vulnerable' due to restricted distribution (less than 20,000 km²; IUCN 2022). Thus, the limited distribution ranges reflect the inherent vulnerability of epiphyte species.

Given the different methods employed to assess endemism, direct comparisons should be made with caution, for example, Fjelds , Lambin, and Mertens (1999) observed that endemic species among Andean birds followed the same pattern as overall species richness distribution and proposed that most endemic species represent relict populations that endured periods of climatic change. Similar hypotheses have been proposed for other groups, such as mammals (Sonne et al. 2022). Noteworthy, it has been suggested that epiphytes can have very small range sizes and high vulnerability to extinction (Le o, Reich, and Nic Lughadha 2023).

The species richness pattern of epiphytes mostly mirrors that of neotropical plant diversity richness, and our study identified several centres of endemic species richness that coincide with global areas of high plant and vertebrate diversity (Kier et al. 2005). Nonetheless, it is known that there is a positive bias in richness and endemism in regions of the moorlands of the Andes, adjacent east-Andean slopes or Amazon lowlands due to shared species between those regions and the use of convex polygons (Leimbeck, Valencia, and Balslev 2004). However, general patterns coincide with those reported in the literature, for example, epiphytes were less common in drier and hotter areas (e.g., the Yucatan peninsula province in Mexico), which can be related to lower water availability (Zotz, Hietz, and Einzmann 2021) and the extremely low and/or high temperatures at subcontinental scales, which are reported to affect epiphyte distribution (Costa Elias et al. 2024). Although some species can tolerate low precipitation or humidity regimes (e.g., atmospheric *Tillandsia*, poikilohydric polypoids; Benzing 1986), epiphyte diversity is concentrated in areas with high and stable water availability (Kreft et al. 2004; Zotz 2016).

The Andean region, including Paramo and Cauca provinces, is one of the important centres of epiphyte diversity and endemism (Gentry and Dodson 1987). This region exhibits great geographical and environmental heterogeneity, resulting in the presence of diverse microhabitats that support numerous species (Gentry 1982; Hoorn, Palazzesi, and Silvestro 2022). The dynamic landscape changes caused by the Andean uplift process have further contributed to the diversification of species (Hoorn, Palazzesi, and Silvestro 2022; Pérez-Escobar et al. 2017). Epiphytic aroids (particularly of the genus *Anthurium*) and orchids are the major contributors to endemic species in the Andes (Givnish et al. 2016; Pérez-Escobar et al. 2017; Reimuth and Zotz 2020). In Central America, the Guatuso-Talamanca and Puntarenas-Chiriquí provinces are the most prominent centres of endemism, the region's importance for species diversity stemming from its location as the point of connection between North and South America after the isthmus formation and the high mountains in the regions, just as for the Andes (Morawetz and Raedig 2007). The Andean region, together with the Guatuso-Talamanca and Yungas provinces, was a significant hotspot for endemic species in the Polypodiaceae family (Suissa, Sundue, and Testo 2021). In addition, Brazil's Rondonia and Atlantic provinces play a crucial role in supporting endemic species (Freitas et al. 2016). Rondonia stands out for its remarkable rates of endemism, particularly among *Peperomias*, while the Atlantic province is notable for its high levels of endemism in bromeliads, attributed to topographic barriers (Freitas et al. 2016; Kreft et al. 2004).

4.3 | Endemism per Family

Environmental conditions and geological events (i.e., the rise of the Andes; Hoorn, Palazzesi, and Silvestro 2022), centres of origin and diversification (Pérez-Escobar et al. 2017), as well as dispersal abilities and biotic interactions (Hartley and Gibernau 2019; Horsley et al. 2015), are reasons typically given to explain patterns of endemism in plant families. For example, the Atlantic and Parana Forest provinces, as well as the Paramo province, were endemism centres for Bromeliaceae.

In the Atlantic and Parana provinces (Brazil), the subfamily Bromelioideae diversified around seven million years ago (Givnish et al. 2011). On the other hand, Central America is the diversification centre of the subfamily Tillandsioideae, but this clade is also present in northern South America, specifically in the Andean region, where its species-specific interactions with pollinators such as hummingbirds may have led to high rates of endemism (Kessler, Abrahamczyk, and Krömer 2020). The observed pattern of endemic species in Bromeliaceae could be due to its relatively recent diversification compared to other angiosperms, combined with the highly heterogeneous landscape.

The spatial distribution of many epiphyte species can also be limited by their dispersal and establishment abilities (Janzen, Zotz, and Etienne 2020; Wagner, Bogusch, and Zotz 2013), which may be the main determinant of differences in the number of endemics between families. A majority of epiphyte species have tiny wind-dispersed seeds or spores (orchids and ferns respectively) or winged or plumed seeds (Tillandsioideae), but there is also a substantial number of species with fleshy fruits (Araceae, Bromelioideae, and *Peperomia*) dispersed by birds, bats and other mammals, such as rodents and monkeys (Benzing 2004; Gentry and Dodson 1987). Large range sizes of epiphytes are expected if the distribution is primarily determined by the degree of dispersal limitation. However, there is also evidence that dispersal limitation is more likely to play a role in species that require specific habitats which may be patchily distributed in the landscapes (Kessler 2010; Peck, Peck, and Farrar 1990).

In the case of orchids, seeds are so tiny that they rely on external sources for germination, often mycoheterotrophic fungi (Dressler 1981). In this case, habitat or microsite limitation may result from the absence of suitable mycorrhizal fungi, which orchids need to provide nutrients, especially as seedlings (Rasmussen and Rasmussen 2009). The degree of specialisation in this orchid–mycorrhizae relationship varies, with implications for orchid distribution and rarity (Jacquemyn et al. 2015). Furthermore, mycorrhizae determine the subset of sites an orchid can colonise within its possible climatic range (McCormick and Jacquemyn 2014). These limitations during germination and establishment can lead to smaller distribution ranges and, therefore, to a higher number of narrow endemic species.

Plant species establishment capacity and distribution patterns are also affected by other factors, including their relationships with pollinators. In some plant lineages, greater height in the canopy is advantageous to attract dispersal agents such as birds or bats that forage in higher strata and cover larger distances (e.g., Araceae; Horsley et al. 2015; Snow 1981). Dispersal in epiphytic *Peperomia* species is epizoochorous, facilitated by sticky fruits (Frenzke et al. 2015), which may contribute to their relatively wide distribution. The ability of fruits to attach to flying vectors can also explain the occurrence of geographically widespread species (Sorensen 1986). Meanwhile, orchids and aroids have strong relationships with insect pollinators, which can influence the patterns of endemism (Díaz-Jiménez et al. 2019; McCormick and Jacquemyn 2014). These plants often have intimate, multispecies relationships with their pollinators, which may limit their distribution to sites with high biodiversity (Pemberton 2010). The distribution and availability of these specific pollinators are critical in maintaining the populations

of many orchids (Reiter, Lawrie, and Linde 2018). Additionally, many insects that pollinate orchids have additional symbioses with other taxa, such as food plants and larval hosts, further complicating their distribution patterns (Reiter, Lawrie, and Linde 2018).

4.4 | Final Remarks

Documenting and understanding range size patterns of epiphytes provides us with historical and evolutionary insights which have immediate implications for conservation (Jetz, Rahbek, and Colwell 2004; Mittermeier et al. 2004). For example, it allows us to identify regions that host a relatively high number of epiphyte species that are potentially vulnerable to anthropic impacts such as land use and climate change due to their reduced range size. Indeed, recently we found that nearly 60% of the studied epiphyte species (6721 species) were threatened, according to IUCN Red List guidelines, and the diversity centres of these species largely coincide with diversity hotspots in Central America, the northern Andes and the Atlantic Forest (Carmona-Higuita et al. 2024). These areas are essential for conservation since the range size is inversely related to extinction risk (Gaston 2003). Narrow-ranged species are more sensitive to disturbance and, therefore, more threatened (Gaston 1994). The centres of epiphyte endemism identified in our study in the neotropics warrant further evaluation and, if necessary, prioritisation for conservation efforts. This is crucial because existing protected areas within certain neotropical regions may be inadequate to effectively safeguard these important biodiversity hotspots and centres of endemism (e.g., Amazon and Atlantic Forest; Sobral-Souza et al. 2018). Therefore, our findings suggest that it is necessary to cross-reference our results with existing conservation areas to determine their conservation value for epiphytes and ensure their long-term protection.

5 | Conclusion

We found that patterns of epiphyte occurrence in the neotropics mostly mirror patterns of neotropical plant diversity since the regions with the highest epiphyte species richness were found in the Andes, Central America and Chocó, as well as in the Brazilian Atlantic Forest and south-west Mexico, and ca. 2400 species (21%) can be called narrow endemics. These results imply that many epiphyte species could be threatened by anthropic disturbances (e.g., habitat fragmentation and loss). Furthermore, the identified centres of endemism should be given high priority for potential conversion into protected areas or for the maintenance of their current protected status. However, it is crucial to assess the representativeness of endemic epiphytes within existing protected areas to gain insights into the current conservation status across the neotropics. Additionally, to enhance the accuracy of these findings, future analyses should incorporate regional herbaria databases and create maps that account for sampling biases and incomplete coverage, which can direct botanical expeditions to under-sampled regions, and lead to the development of comprehensive floras for the identified centres of endemism. These efforts will contribute to a more robust understanding of the conservation importance of these areas and aid in targeted conservation strategies.

Author Contributions

M.J.C.-H., T.K., and G.M.-L. contributed to the study's conception and design. All authors contributed the data for the analysis. M.J.C.-H. performed material preparation, data collection, and analysis. The first draft of the manuscript was written by M.J.C.-H. and reviewed by T.K. All authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Conflicts of Interest

M.J.C.-H declares that she is writing for educational purposes, as this investigation is part of her master's thesis. Therefore, the authors have no relevant financial or nonfinancial interests to disclose.

Data Availability Statement

All data accompanying the manuscript can be found in the Supporting information.

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Supporting Information

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