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RESEARCH ARTICLE

The geographic range size and vulnerability to extinction of angiosperm epiphytes in the Atlantic Forest of Brazil

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Abstract

Aim: Angiosperm epiphytes have long been reported to have larger geographic ranges than terrestrial species, despite evidence of their outstanding diversity and endemism. This apparent contradiction calls for further investigation of epiphytes' poorly understood range size patterns. Here, we address the question of whether epiphytes have larger geographic ranges and different vulnerability to extinction than terrestrial species.

Location: The Atlantic Forest of Brazil, a global centre of tropical epiphyte diversity with relatively well-known flora, where we can estimate the geographic ranges of a large number of species with reasonable confidence.

Time period: Occurrence records from the 17th century to the year 2021.

Major taxa studied: Flowering plants (angiosperms).

Methods: We downloaded, processed and cleaned all occurrence records for the angiosperm species native to the Atlantic Forest of Brazil available in the speciesLink network and the Global Biodiversity Information Facility. We estimated the extent of occurrence and area of occupancy of 12,679 native flowering plants, including 1251 epiphytic species. We compared the geographic ranges of epiphytes and other life forms at broad (e.g. Angiosperms, Monocots) and more restricted taxonomic scales (e.g. individual families), assuming species are independent entities and also when accounting for species phylogenetic dependence.

Results: We found that epiphytes have among the smallest geographic ranges of flowering plants. We found no consistent evidence that epiphytism leads to differences in geographic ranges between close relatives. However, both epiphytes and non-epiphytes in epiphyte-rich lineages have small ranges and likely a high vulnerability to extinction.

Main Conclusions: Our findings contrast with the long-held hypothesis that epiphytes have larger geographic ranges than terrestrial species. Epiphytes and their close relatives share many diversification mechanisms and ecological adaptations ('epiphyte-like traits'), which probably explain why both sets of species have small range sizes and high vulnerability to extinction.

KEYWORDS
epiphytic lineages, extinction risk, geographic distribution, Mata Atlântica

1 | INTRODUCTION

Epiphytes—plants that germinate and grow non-parasitically on other plants—are fascinating components of tropical plant diversity. They comprise roughly 10% of vascular plant species globally, with over 31,000 known species (Zotz et al., 2021), and often reach a higher percentage in the neotropical floras (Taylor et al., 2021). In regions such as the Atlantic Forest of Brazil, 80% of epiphyte species are endemic (Freitas et al., 2016), a substantially higher level of endemism than observed in other plant or animal groups in that region (Ramos et al., 2021).

The macroecology of epiphytes remains poorly understood, despite increasing knowledge of epiphytes' diversity patterns across latitudinal and elevational gradients (e.g. Cardelús et al., 2006; Ding et al., 2016; Hollenbeck & Sax, 2021; Kessler, 2001). In particular, our understanding of epiphytes' geographic range sizes and the underlying evolutionary and ecological mechanisms is limited. The outstanding diversity and endemism of epiphytes might suggest that they would have, on average, small geographic ranges. However, epiphytes have long been reported to have larger geographic ranges than terrestrial species (Schimper, 1888) based largely on studies conducted before the availability of modern large-scale databases of plant occurrence records (e.g. Ibisch et al., 1996; Kessler, 2002; Schimper, 1888), although a recent study focused on the Araceae genus *Anthurium* also supports the claim (Reimuth & Zotz, 2020). This apparent contradiction is intriguing, although rarely highlighted in the literature (but see Kreft et al., 2004), and merits further investigation based on updated sources of evidence. A potential misunderstanding of epiphytes' geographic range size would affect our theoretical understanding of epiphytes' macroecology and misrepresent the perceived vulnerability of epiphytes to extinction in a rapidly changing environment (Köster et al., 2013; Zotz & Bader, 2009).

The geographic range size of species is perhaps the ecological attribute which provides the clearest indication of the species' vulnerability to extinction, underpinning the most commonly used criteria to assess a species as threatened in the IUCN Red List of Threatened Species (Nic Lughadha et al., 2019). Species with narrow ranges are vulnerable to having all their populations simultaneously extirpated by pressures such as habitat loss resulting from land-use changes (Newbold et al., 2018; Staude et al., 2020). Evidence concerning epiphytes and epiphyte-rich taxonomic groups supports this expectation that narrow-ranged species are more vulnerable to land-use changes than widespread species (Köster et al., 2013; Krömer et al., 2019; Vergara-Rodríguez et al., 2017; Zizka et al., 2020).

Two main hypotheses attempt to explain why epiphytes might have larger ranges than terrestrial species. First, the successful colonisation of the canopy would select for long-distance dispersal (Kessler, 2002). For instance, the height provided by tree canopies should benefit the dispersal of dust-like and wind-dispersed seeds (e.g. orchids, Tillandsioideae bromeliads) and fleshy fruits dispersed by birds and bats (e.g. aroids, Bromelioideae bromeliads, *Peperomia*) to greater distances compared to ground level (Einzmann & Zotz, 2017; Fischer & Araujo, 1995; Kessous et al., 2022; Reimuth & Zotz, 2020; Thomson et al., 2011). Second, the stressful and extreme environmental conditions of the epiphytic habitat would require greater eco-physiological plasticity (Ibisch et al., 1996). These factors, independently or in combination, could contribute to a large range size (Schimper, 1888). The wide plasticity hypothesis, along with the idea that most tree species offer similarly adequate substrates for epiphytes (i.e. low host specificity; Ibisch et al., 1996) have been hard to test due to confounding factors such as tree size and age. Thus, the degree of host specificity among epiphytes is still unclear (Wagner et al., 2015). In contrast to the wide plasticity hypothesis, Givnish et al. (2015) suggested that the epiphytic habitat allows for fine niche partitioning, leading to elevated speciation. Epiphytism has been linked with accelerated net diversification rates among orchids and bromeliads, the two largest epiphytic families (Givnish et al., 2014, 2015), which, in turn, may explain small geographic range sizes (Leão et al., 2020). The evolutionary diversification of epiphytic lineages is thus sufficiently extreme that it might in theory even outweigh the effect of dispersal and niche width on species range sizes.

The Atlantic Forest region of Brazil is an ideal scenario to study the geographic range size of epiphytes. The flora is relatively well-known (The Brazil Flora Group et al., 2022) and rich in epiphytes (Ramos et al., 2019, 2021), which allows estimation of the geographic ranges of a large number of species with reasonable precision (for a tropical hyper-diverse ecosystem). With 15,000 known flowering plants, of which at least 1800 are epiphytes (Flora e Funga do Brasil, 2022), the Atlantic Forest flora presents great diversity in which to explore differences between plant life forms. The Atlantic Forest has a long history of human occupation—inhabited by Amerindians for at least 8000 years and occupied by European descendants for 500 years—and has historically been Brazil's most densely populated region, with 70% of the country's human population (Solórzano et al., 2021). The intense land-use changes left a highly fragmented forest (Ribeiro et al., 2009), subject to persistent disturbances (Tabarelli et al., 2004), that nonetheless has 28% of its original cover (Rezende et al., 2018). Specifically, epiphytes are notable as one of the plant life forms with the highest risk of species extinction in the Atlantic Forest (Leão et al., 2014).

Here, we sought to understand how the geographic ranges of epiphytes compare to terrestrial species, and the contribution of epiphytism and evolutionary history to differences in range sizes and vulnerability to extinction. To this purpose, we estimated the geographic ranges of 12,679 native flowering plants in the Atlantic Forest of Brazil, including 1251 epiphytic species. Specifically, we (i) compared the geographic range of epiphytes and other life forms at broad (e.g. Angiosperms, Monocots) and more restricted taxonomic scales (individual families), (ii) tested whether there are phylogenetically independent effects of epiphytism on range sizes and (iii) contrasted the proportion of species with vulnerably small ranges (i.e. extent of occurrence $<20{,}000\,\text{km}^2$, area of occupancy $<2000\,\text{km}^2$) between epiphytes and other plant life forms. We untangled the seemingly contradictory expectation that epiphytes have larger ranges than terrestrial species while showing higher levels of endemism in order to shed light on the extinction risk faced by epiphytes and their close relatives.

2 | METHODS

2.1 | Taxonomic data

We obtained the list of accepted angiosperm species native to the Atlantic Forest of Brazil from ‘Flora e Funga do Brasil’ version 393.300, hereafter Flora of Brazil (Flora e Funga do Brasil, 2022). We used Flora of Brazil as a reference for taxonomy and identification of the epiphytic life form (n.b., classified as epiphytic habitat in Flora of Brazil). All species classified as an epiphyte in Flora of Brazil were considered an epiphyte in this study, even when multiple classifications for the same species were provided (e.g. when a species was also classified as ‘rupicolous’ or ‘terrestrial’). Thus, our classification includes facultative epiphytes but likely not occasional epiphytes. As hemiepiphytic was a distinct class in Flora of Brazil, and we found no clear definition for the classification into this ambiguous life form (Zotz, 2013), we did not add hemiepiphytes to this study to avoid creating an overly heterogeneous group. Our resulting list included 14,773 accepted angiosperm species native to the Atlantic Forest of Brazil, of which 1860 species were classified as epiphytes (i.e. an epiphyte quotient of 12.6%). Ramos et al. (2019) reported a higher proportion of epiphytic species (15%) for the Atlantic Forest of Brazil adopting a more inclusive definition of epiphytes, encompassing hemiepiphytes. The epiphyte classification in EpiList, a global checklist of vascular epiphytes (Zotz et al., 2021), used to estimate epiphyte quotients in Taylor et al. (2021), also includes hemiepiphytes.

2.2 | Occurrence data

We downloaded all occurrence records for the species in our list available through the APIs of the speciesLink network (specieslink.net) and the Global Biodiversity Information Facility (GBIF.org) in September 2021 using the R package ‘Rocc’ version 0.1.0 (Mortara & Sánchez-Tapia, 2021). SpeciesLink returned 3,723,508 entries of 14,115 species, and GBIF returned 1,951,204 entries of 13,658 species. We processed and cleaned these occurrence records following the workflow described in Lima et al. (2021) using the R package ‘plantR’ version 0.1.4 (github.com/LimaRAF/plantR). Our procedure included the standardisation of collection information and formatting of localities, geographical coordinates and taxon names, which integrates fields from different data sources and minimises loss of useful information. Using the detailed gazetteer for Brazil and Latin America included in ‘plantR,’ we added a gazetteer-based coordinate to records which lacked coordinates but included a verified county-level locality description. We performed several validation steps on coordinates and localities to flag outlier occurrences, coordinates not matching the reported country or state, occurrences in the open sea (we kept records near the coast), and records likely from cultivated individuals. We checked the consistency of the flagged issues before excluding undesirable records. This cleaning procedure reduced the combined datasets to 3,659,159 occurrence records (1,874,829 unique) of 13,537 species. The R scripts associated with this procedure are found in the supplementary materials.

2.3 | Geographic range size

We used the cleaned occurrence records to estimate the species' extent of occurrence (EOO, minimum convex polygon) and area of occupancy (AOO, 2 km square grid cell) as estimated in the R package ‘rCAT’ version 0.1.6 (Moat & Bachman, 2020). We estimated both the EOO and AOO because they provide a complementary indication of the species' geographic range and vulnerability to extinction (Gaston & Fuller, 2009). The EOO captures the spread of the occurrences, and we assume it to be linked with the risk that all occurrences of the species could simultaneously disappear from single destructive pressures. The AOO is expected to be better correlated with the species population size and the number of subpopulations, providing additional predictive ability on the species' vulnerability (Gaston & Fuller, 2009). As the sampling density is low for many species, AOO particularly overestimates vulnerability to extinction based on the area thresholds provided by the IUCN Red List Categories and Criteria (IUCN, 2012). Conversely, our EOO-based vulnerability likely underestimates extinction risk. Species with EOO smaller than 4 km^2 were assumed to have EOO of 4 km^2 to avoid outliers based on possibly untrustworthy levels of precision that were left-skewing the data, which affected 325 species (2.6% of the species with range estimates).

2.4 | Data analyses

Finally, we had available for analysis 12,679 species with life form classification and at least one of the geographic range size estimates. Our analyses aimed at testing the hypothesis that epiphytes have larger geographic ranges than terrestrial species from different angles of comparison, including general averages (i.e. assuming species are independent entities, which is relevant for species-level conservation) and contrasts with close relatives (i.e. accounting for species phylogenetic dependence, which is relevant for a rigorous test of the effect of epiphytism on range size). We included other life form categories to provide a richer context for comparison: aquatic, epiphytic, lithophytic and terrestrial. As the range size distribution is right-skewed (i.e. many species with small ranges and relatively few with large ranges), we log-transformed range sizes for a more symmetric and normal distribution. We made inferences based on medians (to account for the skew in the data) and means of log-transformed values—which are more appropriate for comparison across statistical modelling techniques. The means and 95% confidence intervals in the figures allow for a quick and visual evaluation of the statistical significance of differences.

We compared the geographic range sizes between life forms within taxonomic groups and controlling for phylogenetic distances. These comparisons test whether the species ranges differ between close relatives with different life forms. We used phylogenetic generalised least squares to estimate the effects of epiphytism independent of the phylogenetic proximity between species (Symonds & Blomberg, 2014). We used the R package 'phylolm' version 2.6 for all phylogenetic regressions (Tung Ho & Ané, 2014). We used a broadly inclusive reference phylogeny for the phylogenetic analyses, with 353,185 taxa, backbone from the Open Tree of Life version 9.1 and GenBank data for 79,881 taxa ('ALLOTB' phylogeny; Smith & Brown, 2018). Taxonomic names from Flora of Brazil were matched to the Open Tree of Life taxonomy using the function 'tnrs_match_names' in the R package 'rotl' version 3.0.12 (Michonneau et al., 2016). We fitted phylogenetic generalised least squares models to estimate the effect of the number of species per genus and life form on the mean species' geographic range size. We performed model diagnostics and checked residual plots using the R package 'car' version 3.0-7 (Fox & Weisberg, 2019).

3 | RESULTS

The average geographic range of epiphytes is substantially smaller than that of terrestrial species and most life forms of flowering plants in the Atlantic Forest when assuming species are independent entities (Figure 1, Table S1). If you pick a flowering plant species at random in the Atlantic Forest and it is an epiphyte, you can safely expect it to have a geographic range substantially below the average. This statement is true whether measuring the geographic range as the extent of occurrence or area of occupancy. The median extent of occurrence of epiphytes (314,460 km^2) is only 31% that of terrestrial species (1,009,739 km^2) and 35% that of the median for flowering plants in the Atlantic Forest (890,114 km^2; Figure 1). The median area of occupancy of epiphytes (80 km^2) is half of the area occupied by terrestrial species (168 km^2) or by the average flowering plant (156 km^2).

Epiphytes' small geographic ranges affect their vulnerability to extinction. Together with lithophytes, epiphytes stand out by having the highest proportions of species with vulnerably small ranges—that is range size below the threshold of vulnerability adopted by the IUCN Red List of Threatened Species (IUCN, 2012; Figure 2). Twenty-three per cent of epiphytes had a vulnerably small extent of occurrence (95% CI: 21%–25%), in contrast to 15% of terrestrial species (95% CI: 14%–15%). Epiphytes have significantly higher predicted odds of having vulnerably small ranges than terrestrial species: 1.74 (95% CI: 1.5–2) or 3.38 (95% CI: 2.24–5.11) higher odds of having vulnerably small EOO or AOO, respectively (logistic regression, $p \ll 0.0001$).

However, depending on the taxonomic scale investigated, the geographic range of epiphytes may be similar to or even larger than that of terrestrial species (Figure S1). This may partially explain why previous studies focused on selected epiphytic families found that epiphytes have larger ranges than terrestrial species. Under the assumption that species are independent entities, epiphytes have, on average, smaller geographic ranges than terrestrial species at broadly inclusive scales, such as Angiosperms and Monocots (Figure S1). However, within Bromeliaceae and Araceae, epiphytes tend to have larger ranges than terrestrial species. Note that this is true despite epiphytic bromeliads having very small ranges on average (i.e. over 10 times smaller median EOO and less than half of the median AOO of flowering plants). The difference in range size between life forms of bromeliads can be attributed to the extraordinarily small range size of terrestrial bromeliads (Figure S1).

Epiphytism per se is a relatively minor contributor to differences in range size when comparing closely related species and controlling for their phylogenetic distances (Figure 3). On average, there is no significant statistical effect of epiphytism on the range size of flowering plants in the Atlantic Forest (p = ns, for both AOO and EOO, based on phylogenetic regressions on all angiosperms; Figure 3, Table S2). However, epiphytes were associated with larger ranges than closely related terrestrial species within Bromeliaceae and Araceae (Table S2). Again, the geographic ranges of epiphytic bromeliads are indeed very small on average (Figure 3). Thus, differences in range size are likely driven by the extraordinarily small ranges of terrestrial bromeliads. The small range is thus a characteristic of the Bromeliaceae family, not exclusive to the epiphytic species. The same is true for Orchidaceae, where both epiphytic and terrestrial species show, on average, small areas of occupancy, and there is no significant mean effect of epiphytism on range size (Table S2). In contrast, epiphytism seems to be a driver of larger ranges within Araceae, where the AOO of epiphytes is, on average, larger than that of terrestrial aroids and comparable to the mean AOO of flowering plants.

Small range sizes are more closely associated with entire clades where epiphytism evolved rather than with the epiphytic species alone. Species in epiphyte-rich families are predicted to have less than half of the area of occupancy ($\beta = -1.06$, SE = 0.05, t-value = −20.73, $p < 2^{-16}$; phylogenetic regression on $\log_2$-transformed AOO) and less than a quarter of the extent of occurrence of species in the other families ($\beta = -2.14$, SE = 0.11, $t = -18.83$, $p < 2^{-16}$; phylogenetic regression on $\log_2$-transformed EOO; Figure 4). Belonging to an epiphyte-rich family has a stronger influence on range size than being epiphytic or terrestrial.

Note that the evolution of epiphytism is clustered within a relatively small portion of the angiosperm phylogeny. Species in these lineages tend to share much of their evolutionary history and biological traits, whether epiphytic or terrestrial. The two most speciose families of epiphytes account for 86% of the Atlantic Forest epiphytic species: Orchidaceae (1038 spp) and Bromeliaceae (564 spp). The top five families in numbers of epiphytes account for 95% of the epiphytic species (Figure 5).

An outstanding characteristic of the epiphytic clades in the Atlantic Forest is their large number of closely related species with small ranges. On average, genera of epiphytes (i.e. those with

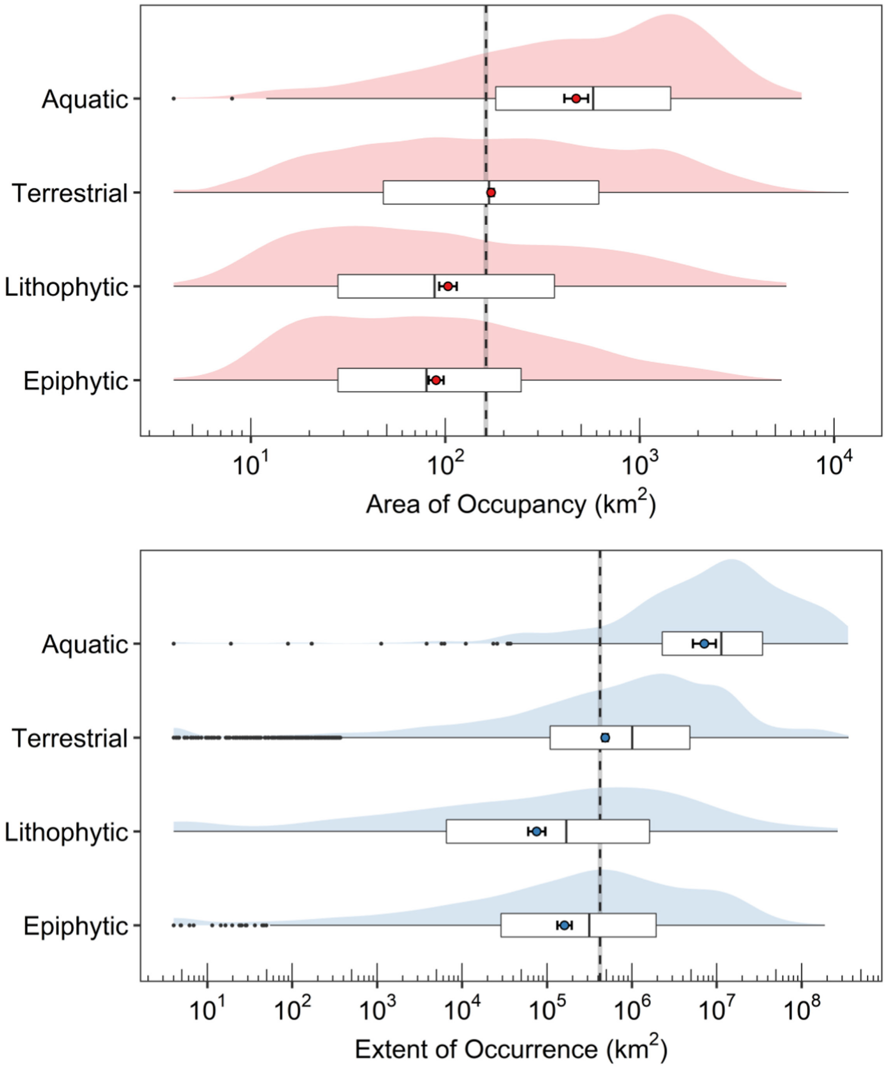

FIGURE 1 Epiphytes have substantially smaller average geographic ranges than terrestrial species and the average flowering plant, assuming species are independent entities. The figure shows, by life forms, the probability densities (coloured background), boxplots (the minimum, first quartile, median, third quartile, maximum and outliers) and means (coloured circles) with their 95% confidence intervals of the area of occupancy and extent of occurrence of 12,679 flowering plant species native to the Atlantic Forest of Brazil. Range sizes are at the $\log_{10}$ scale. The vertical dashed lines and grey areas show the overall mean for flowering plants native to the Atlantic Forest with its 95% confidence interval.

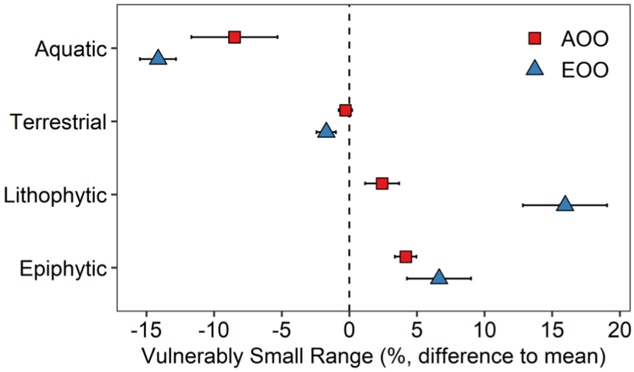

FIGURE 2 Epiphytes have a high percentage of species with vulnerably small ranges (i.e. AOO < 2000 km^2, or EOO < 20,000 km^2; IUCN, 2012) relative to the overall mean of flowering plants (AOO = 94%, EOO = 16%). Error bars show the 95% confidence interval estimated with logistic regressions. Note that the percentage of species with a vulnerably small range is overestimated by AOO due to low sampling density (typical among tropical plants) and likely underestimated by EOO. AOO, area of occupancy; EOO, extent of occurrence.

mostly epiphytic species) have twice as many species as genera composed mainly of terrestrial species (Figure 6; see list of genera in Table S4).

Such unusually large numbers of species (per genus) likely partially explain the species' small geographic ranges and vulnerability to extinction. On average, as the number of species per genus doubles, the mean extent of occurrence reduces by 25% within genera of epiphytes ($\beta = -0.39$, lambda = 0.68, $t = -3.6$, $p < 0.001$) and across angiosperms ($\beta = -0.42$, lambda = 0.54, $t = -11$, $p < 2.2\text{e-}16$; Figure 6).

4 | DISCUSSION

Our results demonstrate that the geographic range of epiphytes is strikingly small compared to the average geographic range of flowering plants in the Atlantic Forest. Epiphytes and lithophytes have the highest proportion of species with vulnerably small ranges among plant life forms, placing them at high extinction risk. However, the small ranges and high vulnerability of epiphytes are typically shared

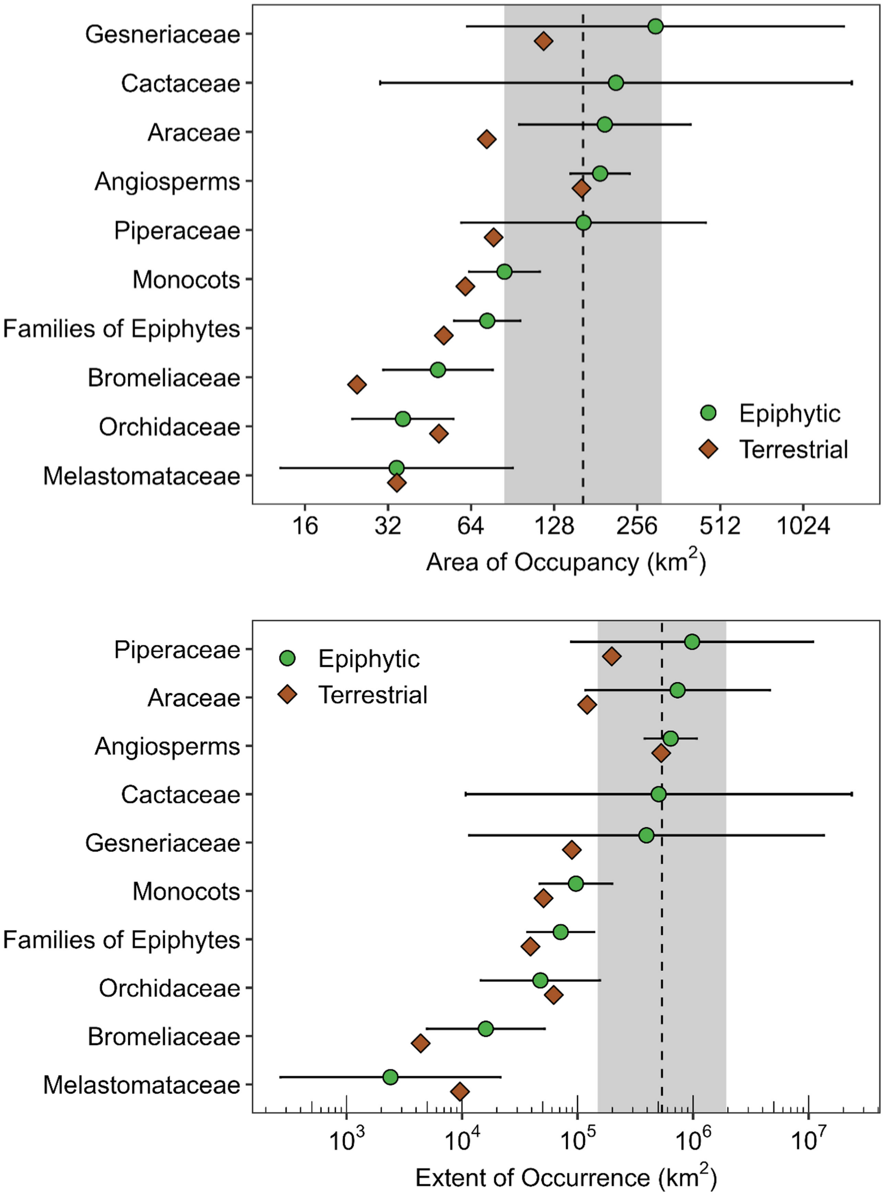

FIGURE 3 Epiphytism per se is a relatively minor contributor to differences in range size when comparing closely related species and controlling for their phylogenetic distances. The figure shows the predicted mean values with 95% CI according to the phylogenetic generalised least square models, having terrestrial as the reference group (thus showing only the mean value for terrestrial). The vertical dashed line and shaded area show the overall mean and 95% CI for flowering plants native to the Atlantic Forest. Epiphytes show statistically significant larger AOO and EOO than terrestrial species in Bromeliaceae, and larger AOO in Araceae, Families of Epiphytes and Monocots. Estimates reflect the statistical correction to account for the phylogenetic distance among species, thus the predicted values differ from those observed in Figure S1. The wide confidence intervals reflect the large uncertainty in the estimates. Please refer to Table S3 for a breakdown of the number of species in each category.

with closely related non-epiphytes, suggesting that the reasons for small geographic ranges apply to entire lineages in which epiphytism evolved.

Our findings contrast with the long-held hypothesis that epiphytes have larger geographic ranges than terrestrial species (Ibisch et al., 1996; Kessler, 2002; Schimper, 1888 but see Kelly et al., 1994). Studies in the Andes largely supported Schimper's hypothesis (Ibisch et al., 1996; within Bromeliaceae: Kessler, 2002), even though epiphytes showed a higher percentage of national or regional endemics than terrestrials among Orchidaceae (Ibisch et al., 1996). In the Atlantic Forest, although epiphytes' average range is larger than closely related terrestrial species within certain restricted taxonomic scales (e.g. Araceae and Bromeliaceae), most often, there are no significant effects of epiphytism among closely related species. In Bromeliaceae, where 564 epiphytic species comprise 61% of the family and 30% of the epiphytic species in the Atlantic Forest, the larger range of epiphytes can reasonably be attributed to the exceptionally small ranges of terrestrial bromeliads, as epiphytic bromeliads have indeed very small ranges (i.e. over 10 times smaller median EOO and less than half of the median AOO of flowering plants). In Orchidaceae, where 1038 epiphytic species comprise 75% of the family and 56% of the epiphytic species in the Atlantic Forest, there are no average differences in the range sizes between closely related epiphytic and terrestrial species. In both Bromeliaceae and Orchidaceae, epiphytes typically display a very small range, which is consistent with their high endemism levels that is 80% of Atlantic Forest epiphytes are endemic to that domain (Freitas et al., 2016; Ramos et al., 2019, 2021), and in stark contrast with the expectation that the level of endemism among epiphytes would not reach the average level of endemism among angiosperms (Ibisch et al., 1996).

The contrasting findings between the literature for the Andean region and our study may be explained by differences in data availability, in addition to differences in patterns of epiphytic range size

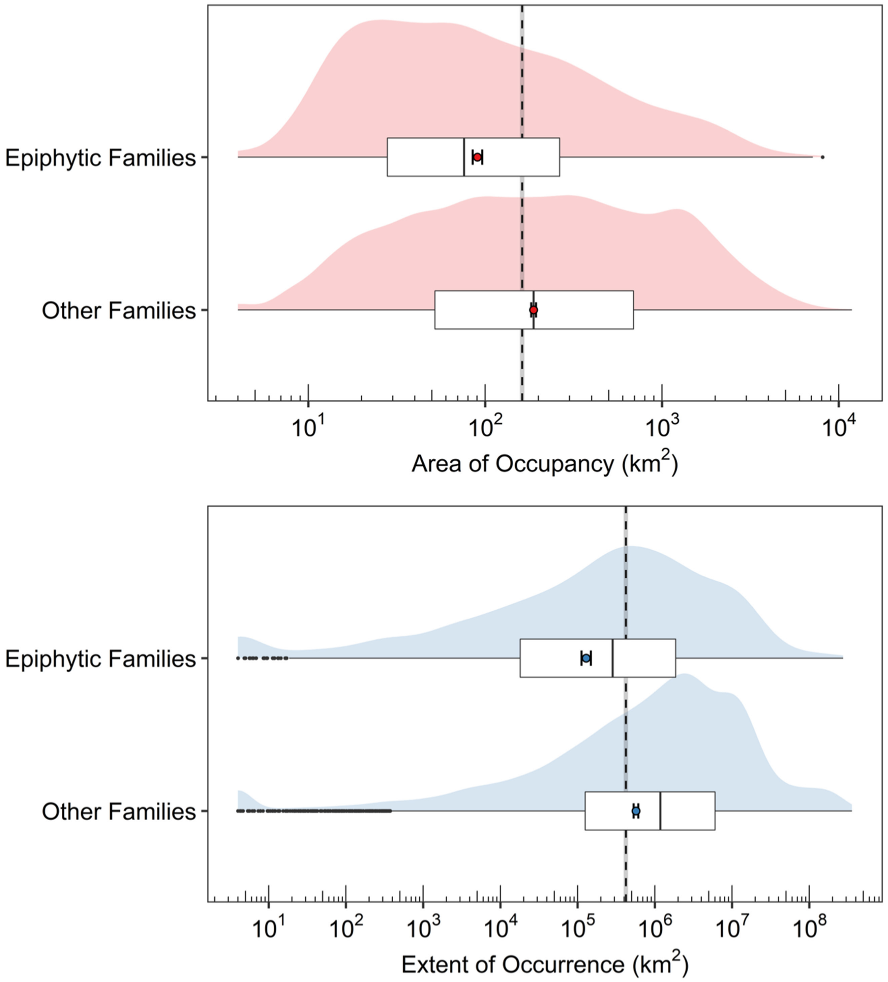

FIGURE 4 Species in epiphyte-rich families have on average smaller geographic ranges than species in the other families. Ridgeline plots show the frequency distribution of the area of occupancy and extent of occurrence of flowering plants of the Atlantic Forest of Brazil in epiphytic families (2576 spp) and other families (10,103 spp). Epiphytic families include the top seven families in numbers of epiphytic species (accounting for 98% of the epiphytic species, Figure 5): Orchidaceae, Bromeliaceae, Piperaceae, Cactaceae, Gesneriaceae, Melastomataceae and Araceae. Range sizes are transformed at the $\log_{10}$ scale. The figure shows the probability densities (coloured background), boxplots (the minimum, first quartile, median, third quartile, maximum, and outliers) and means (coloured circles) with their 95% confidence intervals. The vertical dashed lines and grey areas show the overall mean for flowering plants native to the Atlantic Forest with its 95% confidence interval.

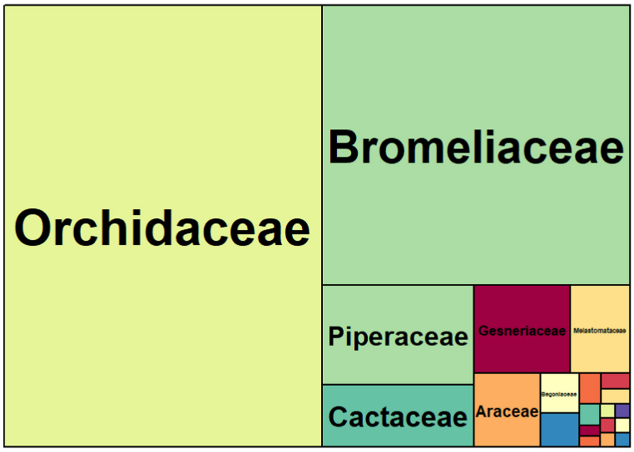

FIGURE 5 Epiphytes are clustered within a relatively small number of families. Treemap of the distribution of epiphytic species across families of angiosperms in the Atlantic Forest of Brazil. The two families that have most epiphytic species include 86% of the epiphyte species: Orchidaceae (1038 spp) and Bromeliaceae (564 spp). The next largest families by the number of epiphytic species are Piperaceae (76 spp), Cactaceae (51 spp), Gesneriaceae (46 spp), Melastomataceae (28 spp) and Araceae (25 spp). Together, these top seven families include 98% of all epiphytic angiosperm species.

between the Andean and the Atlantic Forest regions. For instance, evidence from Ibisch et al. (1996) is based on species endemism to Peru, whereas we calculated the species' geographic range sizes from occurrence records, a more precise estimate of their distribution area. Our study builds on millions of digitally-available occurrence records for the entire taxonomic spectrum of angiosperms, which were not available decades ago. We thus capture a higher proportion of the rare species—which include most of the recently described species—and estimate the small ranges at higher resolution. Logically, the average range sizes will be smaller when capturing more rare species.

An outstanding feature of epiphytic lineages in the Atlantic Forest that helps to explain their small geographic ranges is their large number of species. Lineages with larger numbers of species tend to have species with smaller ranges in the Atlantic Forest (Leão et al., 2020). As we show here, genera with mostly epiphytic species have twice as many species as genera of terrestrial species, consistent with the expectation that epiphytic lineages have high net diversification rates (Gentry & Dodson, 1987; Givnish, 2010; Givnish et al., 2015; Gravendeel et al., 2004; Silvera et al., 2009), but contradicting Ibisch et al. (1996). Elevated speciation rates in the two most prominent epiphytic families (i.e. orchids and bromeliads) are correlated with epiphytism, highly specialised pollination,

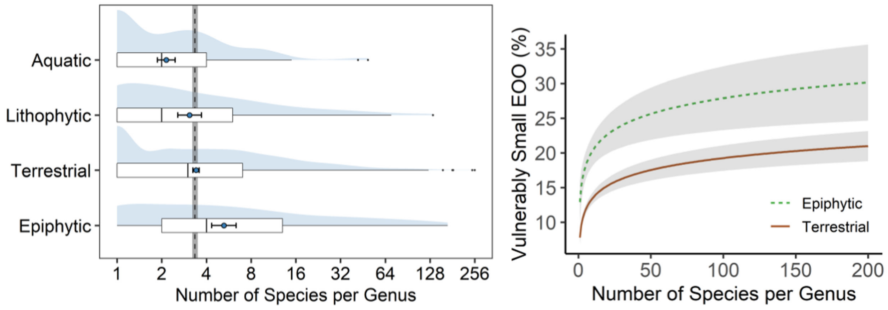

FIGURE 6 Genera of epiphytes have a substantially larger number of species than other genera, and such a large number of closely related species helps to understand the rarity and vulnerability of epiphytes. On the left: Frequency distribution of the number of species per genus across life forms of flowering plants in the Atlantic Forest of Brazil. The figure shows the probability densities (coloured background), boxplots (the minimum, first quartile, median, third quartile, maximum, and outliers), and means (coloured circles) with their 95% confidence intervals. The vertical dashed line and shaded area show the overall mean and 95% confidence interval for flowering plants of the Atlantic Forest. Number of species is in the $\log_2$ scale. On the right: Predicted percentage of species with the extent of occurrence smaller than the threshold of vulnerability (i.e. <20,000 km^2) as a function of the number of species per genus and life form. Shaded areas show the 95% confidence interval calculated from ordinary least squares regression using genus-averaged data. Data includes 1770 genera and 12,679 species.

CAM photosynthesis, and colonisation of tropical montane habitats (Givnish et al., 2014, 2015). Lineages of epiphytes seem especially prone to local speciation, a mechanism of diversification that generates a large number of sympatric species with very small range sizes (Gentry & Dodson, 1987; Givnish et al., 2015). The pattern of local speciation is likely a key driver of the small species' geographic range sizes observed in lineages where epiphytism evolved.

Closely related epiphytes and non-epiphytes share many attributes, which may explain why the small range (and consequent high vulnerability) is similar across entire clades within epiphytically dominant clades, rather than just the epiphytic species. The rapid diversification in these lineages may exacerbate their evolutionary inertia and shared attributes, as closely related epiphytes and non-epiphytes have little divergence time (Givnish et al., 2014). Key ecological adaptations among epiphytes, such as drought tolerance, ability to anchor on an impenetrable substrate, and absorption of water and nutrients directly from the atmosphere, are, to varying degrees, adaptations among non-epiphytes in epiphyte-rich lineages (Zotz, 2016). For instance, the shared adaptive traits between epiphytes and lithophytes likely explain floristic affinities between forest canopies and rocky outcrops (Barthlott & Porembski, 2000; Porembski et al., 1998). Similar ecological tolerances are also needed to colonise nutrient-poor and drought-prone marginal terrestrial habitats such as the sandy coastal plains of the Atlantic Forest (i.e. restingas; Scarano, 2002). It is not uncommon to observe epiphytic species growing facultatively in rocky or terrestrial habitats (Porembski & Barthlott, 2000; Zotz, 2016). Given all the above, the distinction between epiphytes and lithophytes or terrestrial species in epiphyte-rich lineages is often ill-defined, making an unambiguous classification challenging (Zotz et al., 2021).

Amplifying the conservation concerns resulting from the small range size of epiphytes and their close relatives is the fact that they also have slow life histories. Epiphytes are inherently slow-growing organisms, with consequences for their population growth and ability to colonise new host trees (Bartels & Chen, 2012; Einzmann et al., 2021; Laube & Zotz, 2003; Mondragón et al., 2015; Schmidt & Zotz, 2002). Epiphytes require a relatively long time to recover their original population size after disturbances such as deforestation and overharvesting (Einzmann et al., 2021; Köster et al., 2013; Mondragón, 2009). On continuously disturbed small fragments of secondary forest in the Atlantic Forest (Tabarelli et al., 2004), species with slow life histories are particularly vulnerable to decline and eventually disappear, as was observed among trees (Laurance et al., 2006), and is likely happening to epiphytes (Köster et al., 2013; Parra-Sanchez & Banks-Leite, 2020)—but see Larrea and Werner (2010). In fact, epiphytes show exceptionally high extinction risks in the Atlantic Forest, which can only partially be explained by their small geographic range sizes (Leão et al., 2014). The combination of small range size and slow growth presents serious concerns for conservation, making epiphytes and their close relatives with 'epiphyte-like traits' highly vulnerable to extinction in a rapidly changing environment.

AUTHOR CONTRIBUTIONS

Tarciso C. C. Leão conceived the initial idea with support from Peter B. Reich and Eimear Nic Lughadha. Tarciso C. C. Leão compiled and analysed the data. Tarciso C. C. Leão wrote the initial draft of the manuscript with contributions from Eimear Nic Lughadha and Peter B. Reich. All authors contributed to developing the ideas, inferences and revising the manuscript.

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CONFLICT OF INTEREST STATEMENT

None.

DATA AVAILABILITY STATEMENT

The R scripts and data needed to reproduce our results are provided as supplementary materials.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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