Climbing mechanisms and the diversification of neotropical climbing plants across time and space

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Summary

- Climbers germinate on the ground but need external support to sustain their stems, which are maintained attached to supports through modified organs, that is, climbing mechanisms. Specialized climbing mechanisms have been linked to higher diversification rates. Also, different mechanisms may have different support diameter restrictions, which might influence climbers' spatial distribution.
- We test these assumptions by linking climbing mechanisms to the spatiotemporal diversification of neotropical climbers. A dataset of climbing mechanisms is presented for 9071 species. WCVP was used to standardize species names, map geographical distributions, and estimate diversification rates of lineages with different mechanisms.
- Twiners appear concentrated in the Dry Diagonal of South America and climbers with adhesive roots in the Chocó region and Central America. However, climbing mechanisms do not significantly influence the distribution of neotropical climbers. Also, we found no strong support for correlations between specialized climbing mechanisms and higher diversification rates.
- Climbing mechanisms do not strongly impact the spatiotemporal diversification of neotropical climbers on a macroevolutionary scale. We argue that the climbing habit is a synnovation, meaning the spatiotemporal diversification it promotes is due to the sum effect of all the habit's traits rather than isolated traits, such as climbing mechanisms.

Introduction

Climbing plants can be defined as plants that germinate on the ground and, after a certain point in their lives, cannot mechanically sustain their stems without the help of an external support (Acevedo-Rodríguez *et al.*, 2015 [onwards]; Sperotto *et al.*, 2020). The climbing habit has arisen several times in many distinct plant lineages throughout their evolutionary history (Gentry, 1991; Schnitzer & Bongers, 2002), probably as a convergent response to competition for light in areas where the potential for vegetation growth is higher (Castellanos, 1991; Gianoli, 2015). The climbing habit consists of a series of morphological and anatomical adaptations (Angyalossy *et al.*, 2015), including numerous strategies to climb onto and attach to their supports. These strategies, referred to as climbing mechanisms, involve the behavioral or structural modification of organs such as roots, stems, leaves, or inflorescences in order to climb (Darwin, 1865; Bell, 1991; Isnard & Silk, 2009; Sperotto *et al.*, 2020). Some of the most easily recognizable ones are tendrils, twining stems, and adhesive roots (Bell, 1991), but less common ones include

twining petioles, prehensile branches, and scrambling (Putz, 1984; Durigon *et al.*, 2014; Sperotto *et al.*, 2020). Climbing mechanisms can be divided into active and passive (Sperotto *et al.*, 2020) and can be either complex and specialized traits, with multiple developmental origins (Sousa-Baena *et al.*, 2018), or simple in that they involve relatively little modifications to the plant's body (e.g. large xylem vessels; Sperotto *et al.*, 2020). Climbing mechanisms are often taxon-specific (Hegarty, 1991; Burnham & Revilla-Minaya, 2011) and, therefore, useful characters for the identification of families, genera, and even species.

A few hypotheses have associated specific climbing mechanisms with how climbing plants diversify in time and space. For instance, Gentry (1991) proposed a hypothesis that clades with more specialized climbing mechanisms would have higher rates of diversification, based on the observation that certain neotropical lineages bearing tendrils (e.g. Cucurbitaceae, Passifloraceae, and Sapindaceae) tend to be more species-rich than those presenting other types of climbing mechanisms. Tendrils are sensitive structures of different ontogenetic origins (Sousa-Baena *et al.*, 2018) and are often considered the most specialized

climbing mechanism because they are used exclusively for climbing (Darwin, 1865; Font-Quer, 2001). That is, while the modified stems of twiners are also responsible for conducting water and nutrients – as do stems in self-supporting plants – and prehensile branches and petioles still have the function of supporting leaves, tendrils do not provide any other function for the plant except climbing. Gentry, however, did not propose specific mechanisms (Donoghue & Sanderson, 2015) for how tendrils would lead to faster diversification rates in climbing plants, and his observation was later also challenged by the fact that of the 11 neotropical families with a major climbing plant component (Apocynaceae, Fabaceae, Convolvulaceae, Araceae, Bignoniaceae, Malpighiaceae, Sapindaceae, Passifloraceae, Ericaceae, and Rubiaceae), only four present tendrils (Fabaceae, Bignoniaceae, Sapindaceae, and Passifloraceae), and of the 10 most species-rich climbing genera globally (*Dioscorea, Ipomoea, Calamus, Passiflora, Cissus, Mikania, Rhynchosia, Smilax, Combretum,* and *Jasminum*), only three have tendrils (*Passiflora, Cissus,* and *Smilax*; Gianoli, 2015).

Spatial structuring is an important modulator of speciation and extinction in plants (Vasconcelos *et al.*, 2022), and the role of climbing mechanisms in the diversification dynamics of climbing plants could be linked to biogeographical consequences of differences in support diameter limitations. The evolution of different climbing mechanisms has arisen from the interaction of climbing plants with the surrounding vegetation (Hegarty, 1991), and different climbing mechanisms might be better suited to climb certain types of supports. For instance, twining has been reported to enable climbers to make use of the largest span of support diameters when compared to other climbing mechanisms (Putz, 1984; Putz & Chai, 1987), except for climbers with adhesive roots or tendrils with adhesive pads, which can climb onto virtually any support independent of their diameter (Putz & Chai, 1987) but have less mobility between supports (Putz, 1984; Hegarty, 1991). Based on this premise, tropical forests with well-structured and closed canopies, where supports with larger diameters are widely available, might favor the survival of climbers with climbing mechanisms such as adhesive roots, and hinder those with mechanisms associated with thinner supports such as tendrils (see also Gianoli, 2015). The general diameter of trellis available to climbers in a habitat can thus act as an ecological filter and constrain whether or not lineages with certain climbing mechanisms can thrive in that habitat (Hegarty & Caballé, 1991; Putz & Holbrook, 1991; Durigon *et al.*, 2014).

Although the climbing habit has been appointed as a promoter of diversification and modulator of distribution in flowering plants when comparing climbing vs nonclimbing groups (e.g. Gianoli, 2004; Couvreur *et al.*, 2015; Xue *et al.*, 2020), hypotheses related to the role of individual climbing mechanisms in these dynamics have not yet been thoroughly explored with comprehensive datasets and in an explicitly evolutionary framework. For example, it is unclear whether distribution patterns based on diameter of support requirements are significant in light of species relationships (Felsenstein, 1985; Donoghue, 1989), given that local species richness often belongs to closely related lineages. Assumptions of differences in diversification rates based solely on

number of species do not consider differences in clade age and the possibility that higher species richness results from longer time for species accumulation (e.g. Schley *et al.*, 2018; Vasconcelos *et al.*, 2019; Nge *et al.*, 2020). Contrasting diversification rates of lineages with distinct climbing mechanisms can contribute to the challenging, yet fundamental, question in evolutionary biology: why have some groups diversified more than others (Magallón & Sanderson, 2001; Wiens & Donoghue, 2004; Onstein, 2019)? Studies of this kind have been hampered by the lack of basic data on traits, phylogenetic relationships, and geographical distribution from the areas where climbing plants have diversified the most, that is, the tropics (Gentry, 1991; Grace *et al.*, 2021; Vasconcelos, 2023).

Here, we review the diversity and geographical distribution of climbing mechanisms in neotropical climbers to explore their role in the temporal and spatial diversification of climbing plants. Hence, we aim to test two hypotheses: that more specialized climbing mechanisms, specifically tendrils, are associated with higher net diversification rates within neotropical climbers; and that the distribution of climbing plants in the Neotropics is significantly influenced by their climbing mechanisms. To that end, we also provide a new dataset of over 9000 neotropical climbing species and their respective climbing mechanisms. This work sheds light on the role of climbing mechanisms in generating the diversity of climbing plants in the Neotropics by taking a time- and space-contextualized macroevolutionary approach, which is fundamental to understanding the emergence of the climbing habit as a whole.

Materials and Methods

Database and taxonomy standardization

The neotropical region comprises an outstanding biodiversity with *c.* 37% of all the described species of seed plants, totaling between 90 000 and 110 000 species (Antonelli & Sanmartín, 2011), with the vast majority of them being angiosperms. It is also a region that holds one of the highest, if not the highest (Richards, 1991), diversities of climbing plants in the world (DeWalt *et al.*, 2015). Considering that, an initial database of 10 891 neotropical climbing plant species was assembled from extensive literature searches of taxonomical indexes (Index Kewensis), regional floras and checklists (e.g. Flora do Brasil 2020 Bolivia Catalogue, Catálogo de Plantas y Líquenes de Colombia, Flora Neotropica), with records later confirmed through analyses of herbarium material. Climbing mechanisms for each species were scored through literature and herbaria specimen examination and followed the classification presented in Sperotto *et al.* (2020; Fig. 1b–h). During climbing mechanism scoring, we also depured the list from spurious data. For detailed information on the assembling, cleaning and climbing mechanism scoring of the initial database, refer to Supporting Information Methods S1.

We then used the RBG Kew's World Checklist of Vascular Plants ('WCVP' from here on; Govaerts, 2022) to standardize the taxonomy of our initial database and keep only accepted

species names, thus excluding synonyms, illegitimate or unresolved names. This filtering process was done in R (R Core Team, 2022) using its base functions and the DPLYR package (Wickham *et al.*, 2019) to filter and match names of both databases using the plant_name_id and accepted_plant_name_id columns of the WCVP dataset. Our final database comprises 9071 species in 785 genera and 97 families that were confirmed to be climbing plants and had their climbing mechanisms scored (Table S1). All analyses performed were based on this final database. We focus on the differential diversity between the major angiosperm lineages (i.e. Superasterids and Superrosids) when presenting some of our results. All scripts and datasets used in the filtering and in subsequent analyses are available in the repository https://github.com/psperotto/climbers.

Diversification rate analyses

To test whether more specialized climbing mechanisms promote higher diversification in neotropical climbing plants, the diversification rates of genera with different climbing mechanisms were contrasted using the method of moments (Magallón & Sanderson, 2001) implemented in the function *bd.ms* of the R package GEIGER (Harmon *et al.*, 2008). This method estimates the net diversification rates of clades considering their extant diversity and the age of their stem or crown group (Magallón & Sanderson, 2001). It also allows us to calculate 95% confidence intervals for estimated species richness of a clade, based on the age of the clade and the background net diversification rate of the group in which that clade is nested (e.g. Nakov *et al.*, 2018). Since the relative contribution of extinction to the diversification process is unknown or hard to estimate (Rabosky, 2010), net diversification estimates were calculated under two different scenarios of fixed extinction fraction (ε): no extinction ($\varepsilon = 0$) and high relative extinction ($\varepsilon = 0.9$). The reasoning behind our choice of diversification estimator (and possible caveats) can be found in the Methods S3.

To select genera that were included in the comparison, we followed two criteria: the genus is mostly composed of climbers; and the genus is mostly distributed in the Neotropics. We defined 'mostly' as being composed of at least 75% of climbing species, but we also tested three alternative cutoffs: 80, 90 and 100% (Fig. S1). In order to select these genera, we divided the number of species per genus contained in our taxonomically standardized final dataset of neotropical climbers by the total number of species for that genus, which was obtained from the WCVP (2022) database. We also excluded a few genera that presented more than one climbing mechanism. We then matched this list of genera with the seed plant phylogeny from Smith & Brown (2018). We extracted ages for neotropical climber genera using functions of the R packages APE (Paradis & Schliep, 2019), PHYTOOLS (Revell, 2012), and PHANGORN (Schliep, 2011). Because many genera of climbers are monotypic or were represented by only one species in the Smith & Brown (2018) tree, thus having no crown age estimates, we used calculations for stem nodes only. To make sure that unrevealed patterns are not being driven by particularities of major groups, we compare results for climbing

genera nested within the major groups of flowering plants Superasterids and Superrosids (Magallón *et al.*, 2015). Finally, we also analyzed genera in the context of their families, in order to test whether a finer scale analysis would yield different results. To that end, we selected the five families with the largest number of genera mainly composed of neotropical climbers (i.e. Apocynaceae, Fabaceae, Malpighiaceae, Bignoniaceae, and Cucurbitaceae) to use as background rates (Fig. S2). In the latter analysis, we included only climbing genera composed of at least 75% of neotropical climbing species.

Analyzing the distribution of neotropical climbing plants

To map the distribution of neotropical climbing plants and the relative proportion of individual climbing mechanisms present in an area, we downloaded the distribution points from GBIF for all species of neotropical angiosperms using the R packages TAXIZE (Chamberlain & Szocs, 2013; Chamberlain *et al.*, 2020) and RGBIF (Chamberlain *et al.*, 2022). We filtered these distribution points for common problems such as centroids, duplicates, and points on the sea using functions of the R packages SP and RASTER (Bivand *et al.*, 2008; Hijmans, 2022). Finally, we also filtered the distribution to include only points occurring within the Neotropics *sensu stricto* (from latitudes 23.5 N to 23.5 S) and used the TWGD shapefiles of the WCVP dataset to exclude points that were not in the natural distribution for each sampled genus. We were able to keep distribution points for an average of 75% of species presenting each climbing mechanism in the dataset (Table S2).

To visualize the spatial distribution of climbing plants with different climbing mechanisms, we built maps with the proportion of climbing species in relation to all angiosperms in the Neotropics, as well as maps with the proportion of climbing species presenting each climbing mechanism in relation to all climbers (Fig. 2). The maps were made using the R package MONOGRAPHAR (Reginato, 2016) and a modified version of the hybrid shapefile for neotropical areas from Antonelli *et al.* (2018). The original shapefile contained 10 areas, each area classified as either 'Open/Dry', 'Forested/Wet' or 'Mixed' by the authors. For our mapping, we merged together all areas under the same classification, thus leaving three larger areas instead of the 10 in the original shapefile. In that way, we were able to visualize the relative distribution of each climbing mechanism in relation to the type of habitat where they occur.

Closed canopy vegetations like tropical forests tend to be associated with higher humidity and water availability (Toledo *et al.*, 2011; Lines *et al.*, 2012) than more open vegetations like those in the South American Dry Diagonal (Neves *et al.*, 2015), for example. As climatic variables influence the structure of vegetation, they might also influence the distribution of climbing plants based on the putative support requirements of different climbing mechanisms (Hegarty, 1991). To further test whether the distribution of lineages with different climbing mechanisms is influenced by the surrounding vegetation type, we analyzed the potential for vegetation growth inferred from the distribution of each climbing species. To this end, we overlaid the filtered

distribution points with the 30 s arc layer for a Global Aridity Index (AI) dataset (Trabucco & Zomer, 2018) and extracted and summarized mean values for each species using functions of the R packages RASTER (Hijmans, 2022) and SP (Pebesma &

Bivand, 2005; Bivand *et al.*, 2008). Aridity Index values vary from 0 to > 1.5, where lower values are more arid and values above 0.75 are considered hyper-humid areas. By using this information, we test whether species with different climbing
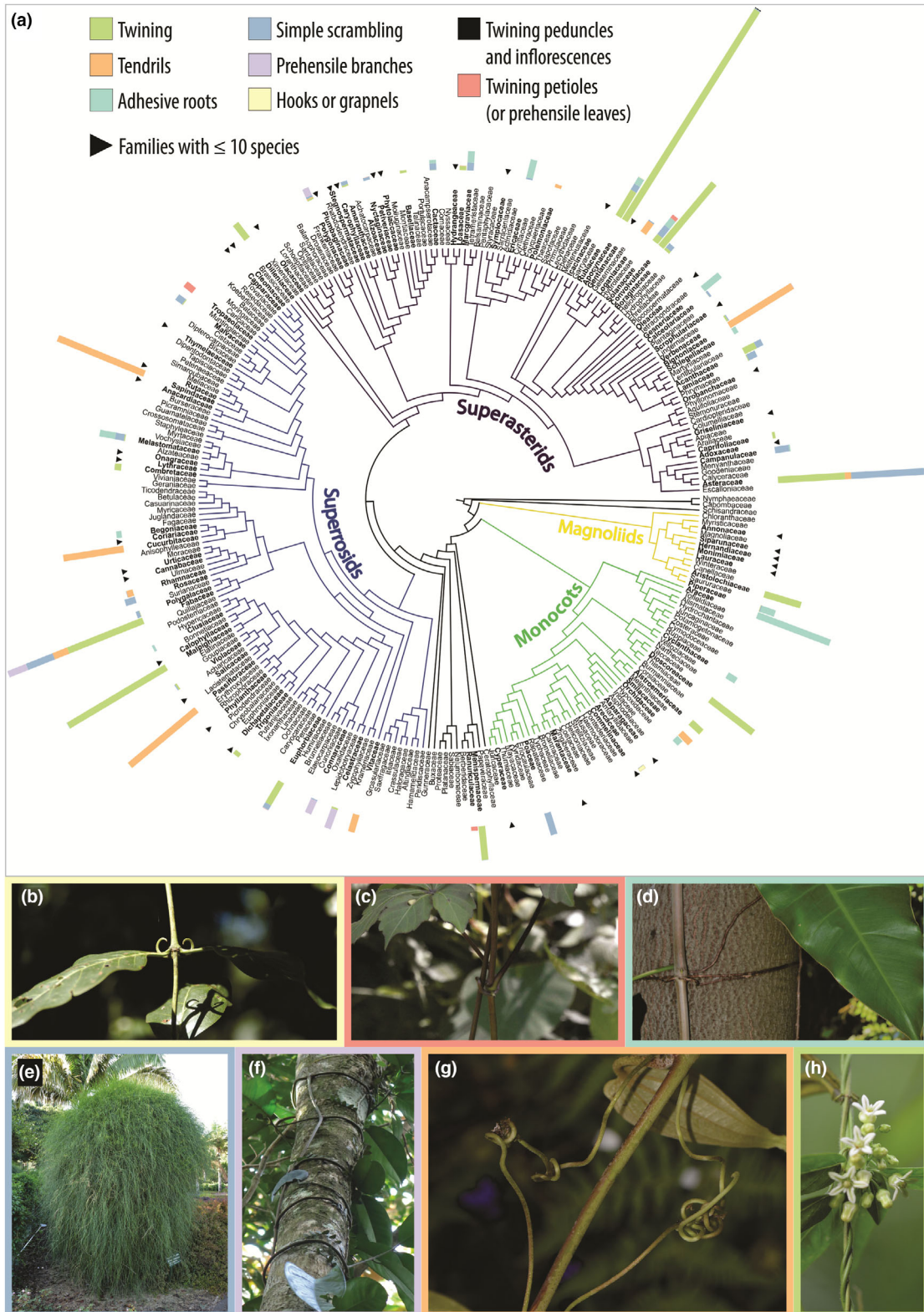
Fig. 1 Diversity of climbing mechanisms in neotropical angiosperms. (a) Phylogeny of neotropical angiosperm families (following APG IV, 2016; details in Supporting Information Methods S2). Major angiosperm clades are highlighted in different colors. Families presenting climbing species are labeled in bold. Bars represent the climbing species richness for each family and are proportional to the number of species presenting different climbing mechanisms within that family. Families marked with a black triangle have 10 or less species of climbing plants. (b–h) Climbing mechanisms of neotropical climbers. (b) Hooks/ Grapnels (*Uncaria guianensis* (Aubl.) J. F. Gmel. – Rubiaceae); (c) Prehensile petioles (*Hidalgoa ternata* La Llave – Asteraceae); (d) Adhesive roots (*Philodendron* sp. – Araceae); (e) Scrambling (*Ephedra tweedieana* C. A.Mey. – Ephedraceae); (f) Prehensile branches (*Peritassa* sp. – Celastraceae); (g) Tendrils (*Smilax* sp. – Smilacaceae); (h) Twining (*Metastelma parviflorum* (Sw.) Schult. – Apocynaceae). The mechanism 'Twining peduncles and inflorescences' is not represented in the figure, please refer to Fig. 5(c,k) of Sousa-Baena *et al.* (2018). Photos by: P. Sperotto (f) and P. Acevedo-Rodríguez (a, b, c, d, e, g, h).

mechanisms are distributed in areas with significantly different AI values, using phylogenetic comparative methods (see below). For more details on the AI, refer to Methods S4.

Phylogenetic comparative methods

Testing for significant differences between net diversification rates and AI values among genera and species with different climbing mechanisms requires considering common ancestry among lineages in the analyses (Felsenstein, 1985). To account for phylogenetic relationships in these comparisons, we pruned the Smith & Brown (2018) seed plant phylogeny built with molecular data (GBMB.tre) to include only species of neotropical climbers with trustworthy occurrence points, finding a total of 1271 matches. We then further matched the same phylogeny with the list of genera of neotropical climbers and kept only one representative per genus in the tree, resulting in a genus level time-calibrated tree of neotropical climbers with 171 tips. We used the genus- and species-level pruned trees to run phylA-NOVA analyses, using functions in the R package PHYTOOLS (Revell, 2012). We aimed to test, respectively: whether lineages with more specialized climbing mechanisms, that is, tendrils, have higher net diversification rates through time than lineages with other climbing mechanisms; whether lineages with different climbing mechanisms are distributed in areas with significantly different AI values, therefore having access to supports with different diameters. Aridity Index and net diversification were treated as continuous characters in each case, whereas climbing mechanisms were treated as a discrete trait in both analyses. Both AI and net diversification rates were log-transformed before analyses, and a significance value of $P < 0.05$ was assumed.

Results

Overall diversity of climbing mechanisms in the Neotropics

The family with the highest diversity of climbers in the Neotropics is Apocynaceae with 1228 species. Together with Asteraceae (728), Fabaceae (712), Malpighiaceae (561), Sapindaceae (459), Passifloraceae (426), Convolvulaceae (406), Araceae (382), Bignoniaceae (367), and Cucurbitaceae (299), these 10 families account for 5568 species, that is, 61% of the total of neotropical climbers (Fig. S3a). The 10 most species-rich genera of climbers were *Passiflora*, with 421 species, *Mikania* (309), *Dioscorea* (267), *Serjania* (238), *Ipomoea* (232), *Philodendron* (200), *Aristolochia*

(186), *Paullinia* (183), *Matelea* (168), and *Heteropterys* (124) (Fig. S3b). Together, these genera sum 2528 species, which is *c.* 27% of all neotropical climbers.

Twining is the climbing mechanism in almost 50% of all neotropical climbers, being observed in 4291 species, followed by tendrils (1931), simple scrambling (1333), adhesive roots (1062), prehensile branches (322), twining petioles (103), hooks and grapnels (26), and twining peduncles or inflorescences (3) (Fig. S4). However, when considering solely the 40 families with 10 or less climbing species, simple scrambling becomes the most common climbing mechanism (58% of 164 species). Twiners are present in all major angiosperm clades, although are concentrated in the Superasterids (2322 species, or 54% of twiners; Fig. 1a). Tendril bearers, on the contrary, are found in all major angiosperm groups except Magnoliids and are better represented in the Superrosids (1380 species, or 71% of tendril bearers; Fig. 1a). Prehensile branch climbers are restricted to the eudicots and are also better represented among the Superrosids (Fig. 1a). All three species presenting the least common climbing mechanism, that is, twining peduncles and inflorescences, belong to a single genus, *Pacouria* (Apocynaceae). Although it is the third most common climbing mechanism, simple scrambling is found in the highest number of families, with representatives in 63 out of the 97 total families in the database, followed by twining (43), adhesive roots (25), tendrils (12), prehensile branches (10), prehensile petioles (9), hooks/grapnels (3), and twining inflorescences (1) (Fig. S5).

Diversification rates

The results presented here refer to the main analyses conducted with genera composed at least 75% of neotropical climbing species and the major angiosperm clades Superasterids and Superrosids as background clades. Other results using higher percentage cutoffs (i.e. 80, 90, and 100%), as well as selected families as background clades (i.e. Apocynaceae, Fabaceae, Malpighiaceae, Bignoniaceae, and Cucurbitaceae), did not differ much from our main analyses and can be found in Figs S1, S2, respectively.

Our categorization recognized 111 genera of neotropical climbers with unspecialized mechanisms and 43 with specialized mechanisms, that is, tendrils, totaling 154 genera. Our results also show that, overall, most climbing genera (44 out of 71 in Superrosids and 48 out of 83 in Superasterids) fall within the confidence interval for the expected number of species of clades evolving under the estimated background diversification rate in their respective major groups. Background diversification rates
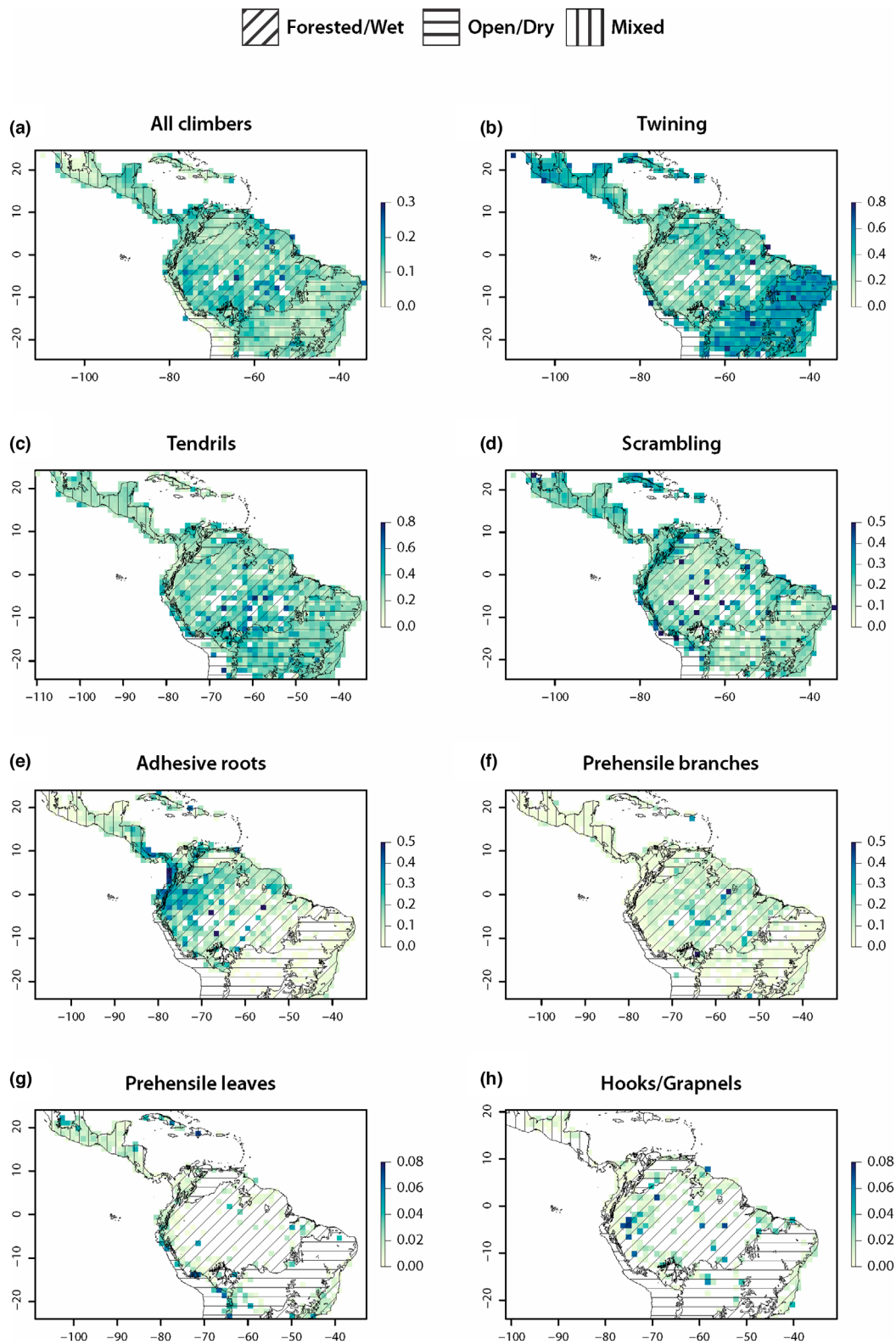
Fig. 2 Distribution maps of species of climbing plants with different climbing mechanisms in the Neotropics. Scales represent proportional species richness (ranging from 0 = 0%, to 1 = 100%). Crosshatched areas follow the area shapefile of Antonelli *et al.* (2018; diagonal: Forested/Wet; horizontal: Open/Dry; vertical: Mixed). (a) proportion of climbing plant species in relation to all angiosperms. (b–h) Proportion of species with each climbing mechanism in relation to all climbing plant species.
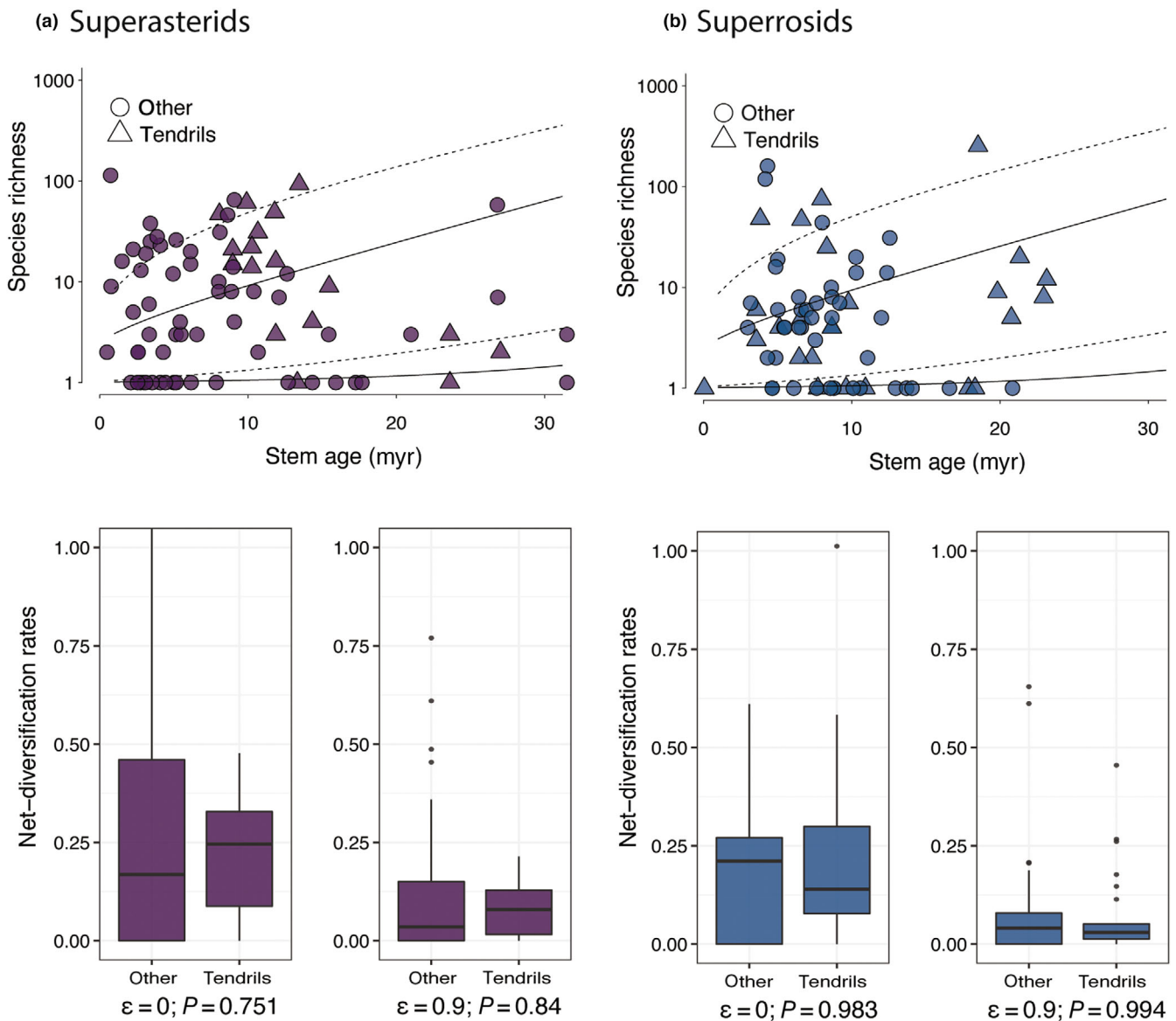
Fig. 3 Diversification analysis. Upper row: confidence intervals of expected species diversity of neotropical climbing genera presenting tendrils (triangles) or other climbing mechanisms (circles; twining, scrambling, adhesive roots, prehensile branches, prehensile leaves, hooks/grapnels or twining inflorescences). The 95% confidence interval of expected species diversity of climbing genera belonging to the Superasterids (a) or Superrosids (b) are presented with net diversification rates of these major angiosperm clades as a background in the absence of extinction (solid lines) and under a high relative extinction rate (dashed lines). Extremely species-rich genera are the ones that fall above the upper limit of the highest confidence interval (i.e. above $\epsilon = 0.9$), while extremely species-poor genera fall below the lower limit of lowest confidence interval (i.e. under $\epsilon = 0$). Lower row: boxplots of phylANOVA pairwise comparisons of net diversification rates between neotropical climbing plant genera presenting specialized climbing mechanisms ('specialist') or others ('all others': either twining, scrambling, prehensile branches, prehensile leaves, hooks/grapnels or twining inflorescences) and belonging to Superasterids (purple) or Superrosids (blue). Black horizontal lines within the boxplots represent median values for diversification rates, upper and lower whiskers represent rates outside the middle 50% values and dots above the whiskers represent outliers. Rates were calculated using the method of moments (Magallón & Sanderson, 2001; see 'Diversification rate analyses' in the Materials and Methods section). P-values for the phylANOVA are presented below the boxes.

were calculated as $0.093 \, \mathrm{r \, myr^{-1}}$ (net diversification events per million year) for Superasterids and $0.091 \, \mathrm{r \, myr^{-1}}$ for Superrosids under $\epsilon = 0$ and $0.075 \, \mathrm{r \, myr^{-1}}$ for Superasterids and $0.073 \, \mathrm{r \, myr^{-1}}$ for Superrosids under $\epsilon = 0.9$. However, in both cases, more clades of climbers appear to fall below the 95% confidence interval line of $\epsilon = 0$ than above the 95% confidence interval line of $\epsilon = 0.9$. That is, more climbing genera (20 out of 71 in Superrosids and 22 out of 83 in Superasterids) appear to be relatively species-poor in relation to the background diversification

rate of their respective major groups. Among the fewer extremely species-rich climbing genera (i.e. genera of climbers that are above the 95% confidence interval, upper dotted line in Fig. 3a,b), Superrosids have proportionally more genera that are tendrilled than the Superasterids: four out of seven genera for Superrosids compared with three out of 13 for Superasterids (Fig. 3a,b, upper row). Tables with genera considered extremely species-rich and extremely species-poor for all percentage cutoffs can be found in the Tables S3, S4, respectively.
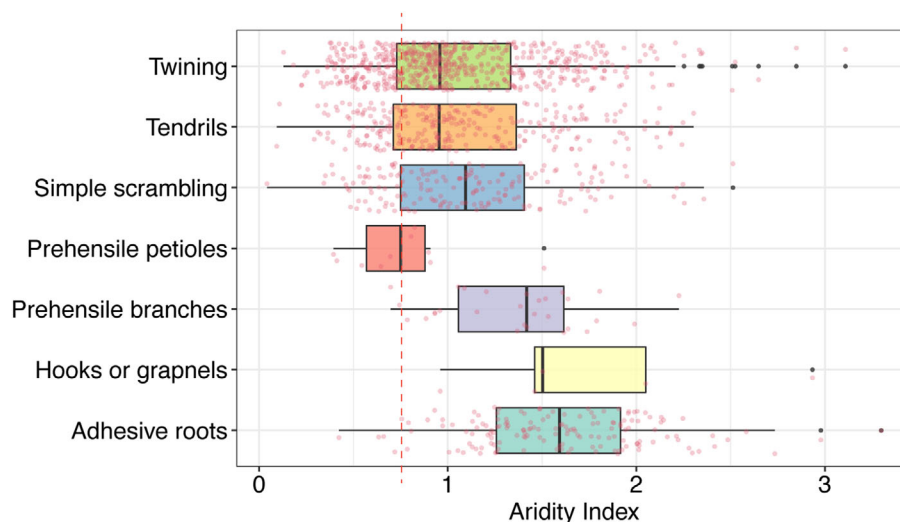
Fig. 4 Boxplots showing different distributions of Aridity Index (AI) values between climbing plants with different climbing mechanisms. phylANOVA pairwise comparisons result in no significant difference between pairs (Supplementary Information Table S5). Boxplots are color coded for different climbing mechanisms and each pink dot represents the mean AI for a species presenting the associated climbing mechanism. Red dashed line indicates AI 0.75, starting values for hyper-humid regions. Black vertical lines within the boxplots represent median AI values, whiskers represent values outside de middle 50% and black dots represent outliers. Sample sizes: Adhesive roots: 152; Hooks or grapnels: 5; Prehensile branches: 29; Prehensile petioles: 10; Simple scrambling: 174; tendrils: 278; Twining: 622.

Results from the phylANOVA pairwise comparisons between lineages with specialized and unspecialized mechanisms show no significant difference between diversification rates in genera of the two groups (Fig. 3a,b, lower row). The median diversification rate for climbing genera with tendrils was 0.14 r myr^{-1} in Superrosids and 0.245 r myr^{-1} in Superasterids, under $\epsilon = 0$. Under the same scenario of fixed relative extinction, climbing genera with all other mechanism presented a median diversification rate of 0.211 r myr^{-1} in Superrosids and 0.168 r myr^{-1} in Superasterids, under $\epsilon = 0$. In analyses fixing $\epsilon = 0.9$, the median diversification rate for climbing genera with tendrils was 0.03 r myr^{-1} in Superrosids and 0.079 r myr^{-1} in Superasterids. This is contrasted to median diversification rates for climbing genera with all other mechanisms of 0.04 r myr^{-1} in Superrosids and 0.035 r myr^{-1} in Superasterids.

Geographical distribution of climbing mechanisms in the Neotropics

The proportion of climbing plant species in relation to all angiosperms for each grid cell in the neotropical region varies mostly from 10 to 20%, with a slightly higher concentration of richness in the southern half of the Amazon (Fig. 2a). Drier regions such as the southwest side of the Andes and the South American Dry Diagonal present a lower proportion of climbers (Fig. 2a). When looking at the proportion of climbers with different climbing mechanisms relative to all climbers (Fig. 2b–h), all mechanisms appear evenly distributed within and throughout the Neotropics, except for twining (Fig. 2b) and adhesive roots (Fig. 2e), where a geographical pattern is clearly observed. Twiners appear to compose between 50 and 60% of the climbing flora in the South American Dry Diagonal, as well as in the northern part of Mesoamerica, where the vegetation is mixed (Fig. 2b). Species with

adhesive roots appear strongly concentrated in Central America around the Panama isthmus and Northwestern South America, particularly the Chocó region in Colombia and Western Amazon, where they compose between 30 and 50% of the climbing flora while being practically absent in all other regions (Fig. 2e).

Environmental factors

The comparison between AI values among species with different climbing mechanisms shows little evidence for differential distribution in habitats with distinct degrees of canopy closure. Median AI for all climbing mechanisms appear above the line of hyper-humid environments (red dashed line, Fig. 4). Adhesive roots appear to be distributed in the highest humidity among all mechanisms (median AI 1.59), followed by hooks and grapnels (1.50), prehensile branches (1.42), simple scrambling (1.09), twining (0.96), tendrils (0.95), and prehensile petioles (0.75). Although we observed that certain climbing mechanisms, such as adhesive roots and twining, appear to be relatively more common in wetter or drier areas (Figs 2, 4), this pattern is not evident when the analysis is corrected for phylogenetic relationship among species (phylANOVA analyses result in $P > 0.05$ for all pairwise comparisons, Table S5).

Discussion

Representation of climbing plants in the neotropical flora

Our state-of-the-art dataset reports the existence of at least 9071 species of climbing plants in the Neotropics. Estimations of the number of vascular plants in the Neotropics range from 90 000 to 110 000 (when only seed plants are considered, Antonelli & Sanmartín, 2011) and possibly up to c. 119 000 (Raven

et al., 2020). Considering that most of these species are angiosperms, that means 7.5–10% of all angiosperm species in the Neotropics are climbers. This overall diversity is not that different from what Gentry (1991) had previously estimated. Here, we found 9071 species composed of 785 genera and 97 families, while Gentry (1991) suggested a total of 9216 angiosperm species of neotropical climbing plants, composed of 584 genera and 96 families (Gentry, 1991). Although we found slightly less species than Gentry (1991), our dataset also includes species in families indicated by Gentry as having climbers exclusively in the Old World: Caryophyllaceae (1), Monimiaceae (1), Oleaceae (5), Rutaceae (1), and Salicaceae (previously 'Flacourtiaceae', 1 sp.) (Gentry, 1991). The considerably larger number of climbing genera in our dataset is probably a reflection of the many taxonomic adjustments and advances in angiosperm systematics of the last 30 yr (e.g. APG IV, 2016).

Regarding the diversity of climbing mechanisms, twining was found to be the mechanism with the largest number of species, whereas simple scrambling was the one appearing in the largest number of families in our dataset. A higher diversity of twiners corroborates a trend that has been consistently shown in previous studies, regardless of geographic region (Putz, 1984; Putz & Chai, 1987; Hu *et al.*, 2010; Durigon *et al.*, 2014; Addo-Fordjour & Rahmad, 2015; Addo-Fordjour *et al.*, 2017), vegetation type (DeWalt *et al.*, 2000; Gianoli *et al.*, 2010; Durigon *et al.*, 2019), or phylogeny (Mohl, 1827; Palm, 1827; Darwin, 1865; Schenck, 1892; Gentry, 1991; Hegarty, 1991). The widespread distribution of simple scrambling in the phylogeny of angiosperms (Figs 1a, S5) indicates that this might be the easiest mechanism to evolve, since it requires little developmental and morphological changes (Sperotto *et al.*, 2020). This is further supported by the fact that this mechanism frequently appears in groups that are not characterized by the climbing habit (e.g. *Croton*, *Mimosa*, *Euphorbia*, *Bidens* and *Vaccinium*, Table S1).

Climbers have been reported as particularly susceptible to undercollection, perhaps because their reproductive structures tend to be restricted to forest canopies (Gentry, 1991; Pandi *et al.*, 2022). Also, they can occupy a large horizontal space throughout the vegetation, emerging from the ground and rooting again many times (Gerwing *et al.*, 2006). The difficulty in discerning ramets (i.e. clonally derived stems) from genets (i.e. genetically distinct individuals; Gerwing *et al.*, 2006), in determining growth form and climbing mechanism, and the problematic terminology associated with the climbing habit (Sperotto *et al.*, 2020), have kept climbing plants off of vegetation inventories. That, and the fact that the number of neotropical climbers seemed to have been stable since the early 1990s, in contrast to a sharp increase in angiosperms in total (Raven *et al.*, 2020), indicates that current datasets of climbing plant diversity, such as ours and the WCVP, may still be underestimating the diversity of climbers in tropical areas. This highlights the importance of revisiting and improving biodiversity surveys within poorly collected tropical areas (e.g. Pandi *et al.*, 2022), where groups tend to be extremely diverse and less well known than in temperate areas (Grace *et al.*, 2021).

Climbers as 'depauperons' and the apparent unrelatedness of specialization and diversification

Regarding the 154 genera composed at least 75% of climbing species, our diversification analysis shows that most (92 out of 154) are within the confidence interval for expected species richness given their stem age and relative to the background diversification rates of their major groups (i.e. Superasterids and Superrosids). Of those that deviate from expected values, most are super-poor genera (i.e. have less species than expected for their stem age) and fewer are super-rich (i.e. have more species than expected for their stem age). This pattern is also seen in the analyses with higher percentage cutoffs (i.e. genera composed at least 80% and 90% of climbing species, as well as 100%), and the higher the threshold, the less genera fell above the upper limit of the 95% confidence interval (Fig. S1). This result indicates that climbing genera tend to be more often 'depauperons' (i.e. species-poor lineages of isolated phylogenetically placement, Donoghue & Sanderson, 2015) than hyper-diverse clades. At least for the neotropical flora, this may appear contradictory to previous analyses showing that the climbing habit promotes diversification (Gianoli, 2004; Couvreur *et al.*, 2015; Xue *et al.*, 2020). However, we note that our study is focused on comparing genera with different climbing mechanisms, and not in comparing lineages of climbers against self-supporting plants. When comparing diversification rates between climbing mechanisms, our results show that genera with tendrils present similar diversification rates as those with other climbing mechanisms, challenging Gentry's (1991) hypothesis that specialized mechanisms lead to faster diversification rates. One could argue that the fact that twiners are far more common than tendrils-bearers (4291 spp. vs 1931 spp., respectively) across neotropical climbers already suggests that the latter might not be a strong diversification driver. Besides, twiners also seem more phylogenetically widespread than tendrils in the neotropical flora, being present in species of 43 angiosperm families, while tendrils appear in only 12 angiosperm families (Fig. S5). Tendrils appear more conserved in groups of higher taxonomic hierarchy, like families (Smilacaceae, Vitaceae, and Passifloraceae) or tribes (Paullinieae and Bignonieae), possibly indicating that they are not easily lost once acquired by a lineage. Examples of these are seen in non-climbing species of *Paullinia* and *Passiflora*, which still produce tendrils, but have lost other characters associated with the climbing habit (P. Acevedo-Rodríguez, pers. obs.). The large number of closely related species bearing tendrils in these clades may have contributed to earlier impressions that this mechanism is associated with higher diversification rates.

Correlations between climbing mechanisms and distribution are dissolved when phylogeny is considered

Climbers in general, regardless of climbing mechanism, appear to represent a higher proportion of the flora in hot and wet biomes in the Amazon and Mesoamerica (Fig. 2a) and to be mainly distributed in hyper-humid habitats (Fig. 4), like tropical rainforests. This distribution pattern is likely related to their anatomy

and vascular systems: climbers invest less in supporting tissues but sometimes hold crowns that are equal in size or even larger than those of large trees (Putz, 1984; Schnitzer & Bongers, 2002). Hence, their stems are built to optimize water and nutrient flux to feed a large crown by using comparatively little space, presenting large xylem vessels (Carlquist, 1991; Angyalossy *et al.*, 2015). The downside of this feature is that climbers, especially lianas (i.e. woody climbers; Sperotto *et al.*, 2020), are more susceptible to vascular damage due to cavitation or embolism caused by exposure to drought and freezing (Tyree & Sperry, 1989; Ewers *et al.*, 1991). Drought-induced embolism might be more easily circumvented by climbers than freezing because they have continuous access to water through their deep roots even in dry seasons (Schnitzer, 2005; but see de Azevedo *et al.*, 2018), but it is still a limiting factor in their distribution if drought is constant.

Additionally, our results show that certain climbing mechanisms appear to be better represented in the climbing flora of certain vegetation types (Fig. 2). Although twiners were thought to better handle the presence of trellis with larger diameters than tendrilled climbers (Putz, 1984), they were found to be counter-intuitively better represented in areas of open vegetation where supports are thinner, such as the South American Dry Diagonal (Fig. 2b). It has been long observed that vines (i.e. herbaceous climbers; Sperotto *et al.*, 2020) are more frequently associated with open environments and forest edges than lianas (Gentry, 1991), allegedly due to their photosynthetic stems and lower susceptibility to drought-induced embolism in the vascular system than lianas (Schnitzer, 2005; Schnitzler *et al.*, 2016; Durigon *et al.*, 2019). Groups of herbaceous climbers tend to produce many small seeds with high abiotic dispersal ability (Grime, 2001), so their establishment in open conditions may be favored. Because many groups of climbers that twine also have a substantial herbaceous component, like Convolvulaceae, Dioscoreaceae, Asclepiadoids (Apocynaceae), and *Mikania* (Asteraceae), a possible explanation for this pattern is that their lack of woodiness is the main driver of their distribution, rather than their climbing mechanism.

Climbers with adhesive roots (i.e. root climbers) appear to be strongly concentrated in Mesoamerica and Northwestern South America (Fig. 2e). Some families whose species predominantly present this climbing mechanism are Araceae, Melastomataceae, Piperaceae, Marcgraviaceae, and Cyclanthaceae (Table S1). These are all families that were listed by Gentry (1982) as being Andean-centered Gondwanan groups, even though the peak of their species richness does not occur in the high altitudes of the northern Andes, but in the wet lowlands and premontane cloud forests along the base and lower slopes of the mountains (Gentry, 1982). These regions present high levels of precipitation, with the Chocó region in Colombia, for example, being one of the wettest regions in the world with up to 10 000 mm (Breña-Naranjo *et al.*, 2015) of annual rainfall. Root climbers have been found to occur more frequently in habitats with higher precipitation and shorter seasonality (Durigon *et al.*, 2013), and the susceptibility of their adhesive roots to desiccation (Hegarty, 1988; Wilder, 1992) is likely the reason why.

The results discussed previously are based on visual analyses of the distribution of climber diversity in the Neotropics (Fig. 2).

However, we note that the correlation between climbing mechanisms and potential vegetation growth is not significant once phylogenetic relationships are considered in the analyses (Fig. 4), and there are two possible explanations for this. First, it might be that potential for vegetation growth as measured by AI is not the best proxy for the availability of supports with different diameters in the area where a climbing species is distributed. Aridity Index was used here as a means to infer general vegetation structure at a broad scale because humidity and potential for vegetation growth are correlated – that is, more humid regions tend to have trees with higher diameters (Toledo *et al.*, 2011; Lines *et al.*, 2012). Yet, AI and tree growth might not be perfectly correlated and this method might not account for other variables that certainly impact the distribution of climbers as well, such as understory vegetation structure. While tropical forests do present some extremely large trees, both in height and in diameter (Richards, 1952; LaFrankie *et al.*, 2006), they also present diverse and structured understory vegetation that can be composed of herbs, shrubs, and treelets (Gentry & Emmons, 1987; Gentry, 1988), all of which have smaller diameters. These act as a trellis and presumably enable climbers with different climbing mechanisms – and, subsequently, different support diameter restrictions – to inhabit such environments.

A second reason is that the patterns of climbers' distribution with different climbing mechanisms may be driven by a few lineages that radiate locally, and not by convergence of the same climbing mechanism in areas with similar AI values. For instance, species with adhesive roots appear to be concentrated in the wettest areas of the Neotropics, but since many of these species are represented by a few families like Araceae and Cyclanthaceae (Leal *et al.*, 2022), their concentration in that area may be a consequence of common ancestry rather than independent events of the evolution of that mechanism (see Vasconcelos, 2023).

Climbing habit as a synnovation rather than a key innovation

Previous hypotheses for how different climbing mechanisms may affect the diversification of climbing plants were mostly descriptive, based mainly on the number of species within clades with specific mechanisms (Gentry, 1991). Although our results show that some mechanisms are indeed more common than others, we found no strong support for significant differences in diversification rates associated with them. Climbing mechanisms appear through evolutionary convergences within the broader framework of the climbing habit. They represent different evolutionary solutions to the same problem – that is, attaching the often slender stems of climbing plants firmly onto their supports. The advantage of one climbing mechanism over the other may be insufficient to impact speciation and extinction rates over time in a significant way. This argument is also supported by evidence that climbing mechanisms are not as relevant to determine species composition of climber assemblages at smaller scales (Seger *et al.*, 2017) and by the fact that it is uncommon that more than one mechanism evolves within the same species, even when they impact different organs (Sperotto *et al.*, 2020).

The evolution of the climbing habit is considered a key innovation in flowering plants (Gianoli, 2004) in the sense of allowing lineages to explore new adaptive zones (Givnish, 2015). The climbing habit is composed of many parts, including anatomical changes in the stem (Angyalossy *et al.*, 2015; Chery *et al.*, 2022), changes in growth rates (Paul & Yavitt, 2011; Wyka *et al.*, 2013), in leaf morphology (Givnish & Vermeij, 1976; Wyka *et al.*, 2013), and in the development of the climbing mechanisms themselves. In that way, we argue that the climbing habit may be better classified as a synnovation (*sensu* Donoghue & Sanderson, 2015) rather than a key innovation. The eco-evolutionary success of climbers was only made possible by the simultaneous presence of all traits that compose the climbing habit, which includes, but is not restricted to, the climbing mechanisms.

Competing interests

None declared.

Author contributions

PS, NR, PA-R and TV conceived the research. PA-R and PS provided the data. PS and TV designed the methods and performed all the analyses. PS, NR, PA-R and TV wrote the manuscript.

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Data availability

All code and datasets necessary to conduct the analyses are available at https://github.com/psperotto/climbers and in the Supporting Information.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Diversification rate analyses of genera with higher cutoffs for percentage of climbing species.

Fig. S2 Diversification rate analyses of genera belonging to five selected families.

Fig. S3 Overall richness of neotropical angiosperm climbing species.

Fig. S4 Barplot of species per climbing mechanism.

Fig. S5 Scatter plot of species per climbing mechanism per family.

Methods S1 Assembling of the initial climbing species database.

Methods S2 Detailing of the construction of the phylogeny presented in Fig. 1 of the main manuscript.

Methods S3 Reasoning behind choosing method of moments as a diversification estimator and caveats.

Methods S4 Details on Aridity Index calculation.

Table S1 List of climbing species and respective climbing mechanisms.

Table S2 Percentage of distribution points per climbing mechanism.

Table S3 Table with extremely species-rich climbing genera.

Table S4 Table with extremely species-poor climbing genera.

Table S5 *P*-values of phylANOVA results for all pairwise comparisons of Aridity Index and climbing mechanisms.

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