

# Climbing mechanisms as a central trait to understand the ecology of lianas across the tropics

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## Abstract

**Aims:** Lianas are a central component of tropical forests. However, how the type of climbing mechanisms is related to the functional and taxonomic diversity of lianas across the tropics, remains largely unresolved. Here, we tested two main hypotheses: (i) the functional diversity of lianas differs with climbing mechanism (active and passive) and (ii) the association between taxonomic diversity with contemporary climate, paleoclimate, forest structure and phylogeny differ between climbing mechanisms.

**Location:** Tropical forests.

**Time Period:** Present.

**Major Taxa Studied:** Terrestrial plants.

**Methods:** We assembled functional traits and the type of climbing mechanism for 702 liana species and used the World Checklist of Vascular Plants (WCVP v.2.0) to standardize species names, map geographical distribution and estimate taxonomic richness. We used kernel density n-dimensional hypervolume to estimate the functional diversity of each type of climbing mechanism. We compared the environmental response of taxonomic richness of each type of climbing mechanism, active and passive, to the response of overall liana species richness. We assessed the magnitude and direction of the environmental response considering variables of climate, soil fertility and forest structure.

**Results:** We found that active climbing exhibits a higher functional richness than passive climbing. Richness patterns of active and passive climbing mechanisms were mainly driven by contemporary climate, paleoclimate and phylogenetic relatedness. More importantly, paleoclimate was negatively associated with active climbing and positively associated with passive climbing.

**Main Conclusions:** Our study highlights differences in functional diversity (richness, dispersion, evenness and originality) between active and passive climbing species, likely reflecting their distinct ecological strategies for resource use, stress tolerance and dispersal. Integrating taxonomic and functional diversity metrics with information about the type of climbing mechanism provides deeper insights into the ecology and response of lianas to climate change.

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## KEYWORDS

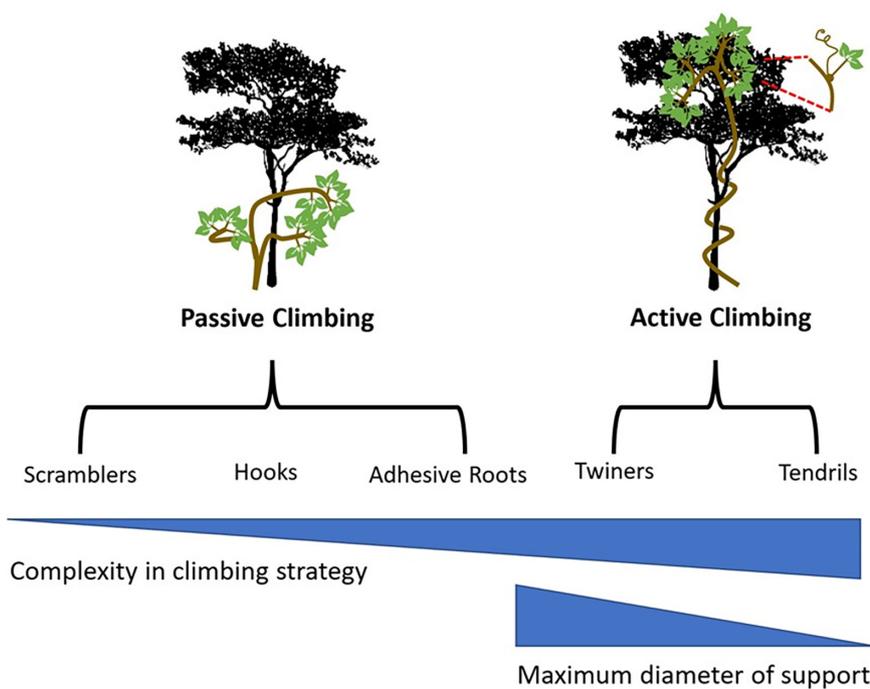
biodiversity, climate change, functional traits, liana ecology, plant life history, tropical forests

## 1 | INTRODUCTION

One of the most eminent changes over the last three decades in tropical forests is the increase in liana abundance and biomass (Schnitzer, 2018; Schnitzer & Bongers, 2011; Yorke et al., 2013). Lianas (woody climbers) are non-self-supporting plants that invest proportionally more in leaf mass than in cross-sectional stem area than trees and therefore must rely on vegetation around as supports to grow and to gain access to the forest canopy (Gerwing et al., 2006; Schnitzer & Bongers, 2002). At least eight studies provide support for increases in liana abundance and/or biomass across Neotropical forests (see Schnitzer & Bongers, 2011). However, studies that have evaluated changes in liana abundance and biomass did not find an increase of lianas in African tropical forests (Bongers et al., 2020; Schnitzer, 2018). An explanation for these inconsistent results could be the differences in species biogeographical distribution and their functional traits. Furthermore, differences in lianas abundances and biomass at larger spatial scales may be driven by climate seasonality (Schnitzer, 2005), soil conditions (van der Heijden & Phillips, 2008) and disturbance dynamics (Schnitzer, 2018). However, why tropical forests across the globe differ in the functional and taxonomic diversity of lianas and the potential role of the climbing mechanisms adopted by lianas in mediating these differences is poorly understood.

Lianas have attracted the interest of botanists because of their distinctive climbing mechanisms and growth strategies (Darwin, 1875; Isnard & Silk, 2009). The vertical growth of lianas

is facilitated via a large diversity of attaching systems (Isnard & Silk, 2009; Rowe & Speck, 2004; Putz, 1984; Speck & Burgert, 2011). For instance, the type of climbing mechanism determines the maximum distance a liana can attain between supports, and climbing success depends on the maximum stem diameter support that lianas can colonize (Isnard & Silk, 2009; Putz & Holbrook, 1991; Rowe & Speck, 2004). In his book 'The climbing movement of plants' (1875), Darwin described hook climbers as having the least efficient climbing mechanism, followed by root climbers, while he considered the more widespread twining and tendril climbers to be the most efficient. However, classifications of the climbing mechanisms used by lianas vary substantially throughout the literature, ranging from three categories (Vaughn & Bowling, 2011) to as high as 10 in some cases (Bongers et al., 2005), as recently reviewed by Sperotto et al. (2020). In this study, we followed the classification of climbing mechanisms proposed by Sperotto et al. (2020) to establish a framework considering two main categories: species with highly specialized attachment systems and the ability to span different host trees (active climbing) and species devoid of highly specialized attachment systems and normally limited to climb on one or few host trees (passive climbing) (Figure 1). Active climbing lianas are plants displaying a support-searching behaviour such as circumnutation and include species with tendril and twiner climbing mechanisms. Instead, lianas with passive climbing do not actively search for support rather they just grow over or lean on their supports, and this group includes species with hooks, scrambles and adhesive roots (hereafter roots) as a climbing mechanism



**FIGURE 1** Framework used in this study. Liana species (woody climbers) may be classified into two main types of climbing on supports: passive and active mechanisms. Each group has different types of strategies. The upper blue arrow indicates an increase in complexity of the type of climbing mechanism from scrambler to tendril. The lower blue arrow indicates an increase in the maximum size (diameter) of the support to which each type of climbing mechanism can attach. Note that the constraint in size of the support is valid only for species with active climbing since species with passive climbing do not climb and pass over different supports.

(Figure 1). Therefore, ecological niche differentiation is evident among liana species employing different climbing mechanisms, as observed by previous studies (Kusumoto et al., 2013; Putz, 1984). For instance, liana species that climb using adventitious roots (passive climbing) typically inhabit the inner, less illuminated areas of the tropical forest canopy (Kusumoto et al., 2013) and display the lowest photosynthetic rates among their temperate counterparts (Carter et al., 1988). Furthermore, tropical lianas with tendrils (active climbing) generally maintain their foliage for shorter durations compared with other liana species with passive climbing from the same environment (Hegarty, 1990) and exhibit a preference for sites with a proliferation of slender supporting stems, thereby tending to specialize in early successional habitats (DeWalt et al., 2000). Despite this evidence, the overall implications of climbing mechanisms for the functional trait diversity of lianas remain so far unexplored.

One emerging question considering the life history of lianas is whether different types of climbing mechanisms are associated with trait syndromes, and coordination among individual traits, reflecting ecological strategies included in a conservative-acquisitive continuum such as the leaf economic spectrum. The theoretical basis for this hypothesis relies on the fact that the type of climbing mechanism limits the maximum size of the support used for vertical growth (e.g., the stem diameter to which a specific climbing mechanism can attach and, consequently, climb on), as well as the light environment that can be explored (Darwin, 1875; Putz & Holbrook, 1991; Putz, 1984). Active climbing species generally have more flexible stems (higher modulus of elasticity) than passive climbing species (Isnard & Silk, 2009; Rowe & Speck, 2015; Speck & Burgert, 2011), which may facilitate higher shoot elongation rates and better access to high-light conditions in the upper canopy for active climbing species (Teramura et al., 1991). However, within the species group with active climbing mechanisms, tendril species are more restricted to attach to trees with smaller diameters than twiners (Putz, 1984; Putz & Chai, 1987); therefore, in forests with high rates of fragmentation or gap formation, where smaller trees dominate, tendril species tend to show high abundance (DeWalt et al., 2015; Letcher & Chazdon, 2009). Moreover, the role of different climbing mechanisms may vary over climate gradients: for instance, while lianas increase in abundance across the tropics peaking in seasonally dry forests (Schnitzer, 2005), root climbers (passive climbing) tended to be more frequent in sites with greater precipitation (Durigon et al., 2013). Despite these observed patterns, to which extent climbing mechanisms relate to trait diversity in lianas, as well as how environmental variables, such as forest structure and climate, influence the species distribution patterns of climbing mechanisms remains answered.

A trait-based perspective considers how ecological and evolutionary dynamics shape the trait space—a multidimensional hypervolume—potentially leading to functional convergence or divergence (Mammola & Cardoso, 2020). Within this context, diversity between groups can be represented by three primary

dimensions: richness, dispersion and evenness, which collectively reflect variation in the trait space (Mammola & Cardoso, 2020; Mammola et al., 2021). At the species level, the position within the trait space can indicate a species' uniqueness/originality and its contribution to overall diversity. Focusing on lianas, dependency on support for vertical growth is a significant filter that may restrict the trait space, favouring functional convergence. For instance, the presence of G-fibres, the wood cells that facilitate stem movement, is common in active climbing species but not in passive climbing species (Chery et al., 2022). Conversely, the forest's vertical heterogeneity, from floor to canopy, presents ecological opportunities for the development of diverse trait combinations, thus facilitating divergence. Despite these insights, the extent to which climbing mechanisms influence functional diversity (richness, dispersion and evenness) in lianas remains poorly understood, posing an important question about the degree of similarity or distinction among lianas based on their climbing strategies.

In this study, we assessed the importance of passive versus active climbing mechanisms for global liana species distributions and for different components of functional diversity at the group level (functional richness, dispersion and evenness) and the species level (contribution and originality) (Mammola & Cardoso, 2020). We, therefore, synthesized data for lianas regarding the main functional traits used to characterize plant form and function and classify the liana species in active and passive climbing (Figure 1—climbing mechanism classification following Sperotto et al., 2020). Furthermore, we integrate the liana species climbing mechanism with a comprehensive global checklist of over 295,000 vascular plant species distributions (Govaerts et al., 2021) to assess the relative importance of active and passive climbing mechanisms to the pattern of lianas taxonomic diversity in different biogeographical regions, and how they are associated with contemporary and paleoclimate conditions, vegetation structure and phylogeny. We tested the following hypotheses:

1. We hypothesize that support dependency, which is the need for external support (e.g., tree or shrub) to grow vertically towards the canopy, is a strong ecological filter to lianas. If so, we expect that active climbing, which has a stronger support dependency demonstrated by its specialized climbing structures, shows higher functional diversity at the group level (richness, divergence and regularity) and the species level (contribution and originality) than passive climbing.
2. The chances to succeed in a specific environment are in part determined by the type of climbing mechanism. We, therefore, expect contemporary climate, paleoclimate climate, vegetation structure and species evolutionary relationships (i.e., phylogeny) to influence the distribution of active and passive climbing species differently. Additionally, we expect that geography will strongly influence the phylogeny of both active and passive climbing, as lianas in general are characterized by a small number of species-rich plant families.

## 2 | MATERIALS AND METHODS

### 2.1 | Functional traits and climbing strategies

We built a trait dataset from peer-reviewed studies and trait information from the BIEN Database (R package 'BIEN' version 4.1.1, Maitner et al., 2018). We found functional traits for 702 liana species: 545 representing active climbing and 157 representing passive climbing. We restricted our analyses to the following functional traits with information available at the species level: individual leaf area (LA), specific leaf area (SLA), foliar nitrogen content per mass ( $N_{\text{mass}}$ ), stem-specific density (WD) and seed mass (SM). We focused on angiosperm woody climbers (lianas). Palm climbers and monocot species, such as *Smilax* spp., were not included, as these groups have different ecophysiological behaviour. In our study, we adopted the liana definition as proposed by Gerwing et al. (2006): 'climbing plants that produce true wood (xylem tissues derived from a vascular cambium) and that germinate on the ground but lose their ability to support themselves as they grow, so they have to rely on external physical support to ascend to the canopy'. Therefore, we did not include species classified as 'hemiepiphyte'. However, we noticed that the criterion of woodiness would exclude some genera of dicotyledons, such as *Passiflora*, *Ipomoea* and many Cucurbitaceae, which have perennial fibrous stems but are abundant and important in many liana inventories (Gentry, 1991; Gerwing et al., 2006). Thus, we have also included in our analyses species from the genera *Passiflora* and *Ipomoea* as well as species from the family Cucurbitaceae. Species showing different classifications for their climbing mechanisms were excluded to avoid uncertainties. We classified each liana species according to a specific type of climbing mechanism through a thorough literature survey. We checked online sources and databases (e.g., virtual herbaria and online floras) to find information about the type of climbing mechanism (Appendix S1). We classified liana climbing mechanisms following Sperotto et al. (2020). We focused on the comparison between the active and passive climbing mechanisms used by lianas. We only included species identified to the binomial level and limited our search to studies reporting the traits of adult plants growing in natural conditions. Therefore, we did not include data from seedlings and saplings or plants growing in experimental conditions. In total, we assembled data from 42 studies encompassing 702 species of lianas, with information for at least one of the above traits for each species (trait coverage can be found in the Support Information—Extended Data 1).

To overcome the limitation of species with missing information for the traits dataset, we used phylogenetic trait imputation as suggested by several studies (Johnson et al., 2020; Joswig et al., 2023; Penone et al., 2014). We built a phylogenetic tree with the R package V.PHYLOMAKER2 (Jin & Qian, 2022) and used the phylogenetic information to impute trait values. Imputation of missing trait values was performed by a random forest algorithm, the missForest function, in the MissForest R package (Stekhoven & Bühlmann, 2012). To assess the predictive accuracy of the algorithm, we used the

out-of-bag error approach. This approach consisted in comparing the random forest approach, which incorporated phylogenetic relationships among species, with an alternative approach that predicts trait values without considering phylogenetic information. Our findings indicated that the phylogenetically informed imputation performed better or equal to the alternative approach for most traits (see Support Information—Extended Data 1). Finally, as closely related species tend to have similar trait values, we estimated the phylogenetic signal for each trait with Pagel's  $\lambda$  using the phylosig function in the R package phytools (Revell, 2012) (Support Information—Extended Data 1).

As closely related species tend to have similar trait values, we estimated the phylogenetic signal for each trait with Pagel's  $\lambda$  using the phylosig function in the R package phytools (Revell, 2012). We built a phylogenetic tree including all liana species, for this we used the extended version of the Smith and Brown (2018) phylogeny, implemented in the R package V.PHYLOMAKER2 (Jin & Qian, 2022). We estimated the phylogenetic signal before trait imputation.

### 2.2 | Species richness

We used the RBG Kew's World Checklist of Vascular Plants (referred to as 'WCVP' hereafter; Govaerts et al., 2021) to standardize the taxonomy and keep only accepted names in our database by excluding synonyms, illegitimate or unresolved names. Our final database consists of 702 species (Support Information—Extended Data 2) with the type of climbing mechanism scored for each of them. Subsequent analyses were conducted using this final database. Species distributions from the WCVP are recorded at the level of 'Botanical Country' according to the World Geographical Scheme for Recording Plant Distributions (WGSRPD, Brummitt et al., 2001). We estimate absolute species richness for liana species and for each climbing mechanism separately as the number of species within the level of 'Botanical Country' (hereafter region). The total richness of lianas was used to calculate the relative proportion of each climbing mechanism within each region. More specifically, while 'total liana richness' is the sum of all liana species within a region, 'climbing mechanism richness' is the sum of all liana species of a particular climbing mechanism within a region.

### 2.3 | Environmental predictor variables

Since available trees for climbing are important for lianas, we used an index to express forest structure as the product of canopy height by tree density. For each region, we extracted canopy height at 1 km<sup>2</sup> resolution from Simard et al. (2011) and tree density at 1 km<sup>2</sup> resolution from Crowther et al. (2015) and multiplied both values.

To assess how climbing mechanisms are associated with contemporary climate, we selected three bioclimatic variables from CHELSA v.2.1 (Karger et al., 2017) with 30 arc-seconds resolution.

These bioclimatic variables are important in determining plant diversity patterns (Cai et al., 2023; Kreft & Jetz, 2007; Scheiner & Rey-Benayas, 1994): mean annual temperature (°C), mean annual precipitation (mm) and temperature seasonality (coefficient of variation of mean annual temperature). The potential legacy of past climate on each climbing mechanism was tested by calculating the change between the present and the Last Maximum Glacial (LMG) for mean annual temperature and precipitation. The difference between mean annual temperature and precipitation at the present and at the LMG, hereafter referred to as temperature and precipitation anomaly, is calculated for each grid cell and aggregated to the botanical country level. The LMG data for temperature and precipitation were extracted from the PaleoClim database with 30 arc-seconds resolution (Brown et al., 2018).

## 2.4 | Phylogenetic predictor variables

To disentangle the evolutionary and ecological contributions to the patterns of climbing mechanism richness, we calculated region-level phylogenetic eigenvectors as additional predictor variables in our models. First, we constructed the phylogenetic tree with the extended version of the Smith and Brown (2018) phylogeny, implemented in the R package V.PHYLOMAKER2 (Jin & Qian, 2022). We used the phylo.maker function and generated a phylogenetic tree hypothesis under scenario 3 (Jin & Qian, 2022). Although scenario 3 incorporates missing species as polytomies, previous studies have demonstrated the robustness of this approach for large-scale biogeographical analyses (Cai et al., 2023; Qian & Jin, 2016, 2021). In the second step, we calculated phylogenetic turnover (Phyloobs) between regions for each climbing mechanism separately, using the Simpson index due to its insensitivity to variations in species richness between sites (Baselga, 2010). However, similar to the strong influence of species richness on phylogenetic richness, the species compositional turnover also affects the phylogenetic turnover. To overcome this issue, we quantified the standardized effect size of phylogenetic turnover (Phyloses) for each climbing mechanism, accounting for variations in compositional turnover among regions. We calculated the Phyloses by using the PHYLOREGION package in R (Daru et al., 2020). We generated multiple null assemblages by shuffling the tip names in the phylogenetic tree 1000 times for each climbing mechanism separately. With this procedure, we obtained the mean null phylogenetic turnover (Phylomean\_null) and its standard deviation (PhyloSD). Then, we calculated:  $\text{Phyloses} = (\text{Phyloobs} - \text{Phylomean\_null}) / \text{PhyloSD}$ . In a third step, we performed a principal coordinates analysis (PcoA) on the resulting Phyloses distance matrix to create phylogenetic eigenvectors at the regional level. By doing so, we captured the total variation in phylogenetic composition between regions. We used these eigenvectors as predictor variables in our model. With these phylogenetic eigenvectors, we were able to assess how the species' phylogenetic relatedness across regions influences the patterns of climbing mechanism

richness within a given region. We included the first 2 PcoA axes in our models.

## 2.5 | Statistical analysis

### 2.5.1 | Functional diversity metrics

We evaluated how climbing mechanisms may have shaped the functional diversity of lianas by assessing the contribution of active ( $n=545$ ) and passive ( $n=157$ ) climbing species to the overall liana trait space following the approach of Barajas Barbosa et al. (2023) and Mammola and Cardoso (2020). First, to map trait spaces, we performed a principal component analysis (PCA) on the log-transformed and z-transformed (centred and rescaled to unit variance) mean trait values. We performed one PCA using all liana species, and one PCA for each climbing mechanism separately. Then, we used the n-dimensional functional hypervolume approach (Blonder, 2018), which accurately accounts for gaps in the trait space compared with other methods (Villéger et al., 2008). Here, the first three principal components derived from the PCA are used to delineate the hypervolume, and the position of the observations (e.g., species) in this multidimensional space can be used to characterize different aspects of diversity (e.g., richness, dispersion and evenness). To build the hypervolumes, we used the Gaussian method, which exhibits lower sensitivity to bandwidth variation and fits the data loosely. These characteristics are particularly suitable for functional diversity estimation (Blonder, 2018). To assess the overlap between the trait spaces (all liana species combined, active climbing and passive climbing), we first built hypervolumes using the principal components from PCAs run for each individual dataset. We used a fixed kernel bandwidth for each individual dataset, computed through the estimate\_bandwidth function in the R package Hypervolume (Blonder, 2018). For each climbing mechanism, we assessed three components of functional diversity (Figure 3): richness, evenness and dispersion. We used the functions kernel.alpha, kernel.evenness and kernel.dispersion from the R package BAT (Mammola & Cardoso, 2020) to estimate richness, evenness and dispersion, respectively. Functional richness measures the total volume of a trait space (the hypervolume). Functional dispersion measures how spread, or dense, a given trait space is, by calculating the average difference between the centroid and species (points) randomly placed within the boundaries of the hypervolume (Mammola & Cardoso, 2020). Functional evenness measures the regularity of a trait space by calculating the overlap between the observed hypervolume and a theoretical hypervolume, where traits and abundance are evenly distributed within the total trait space (Mammola & Cardoso, 2020).

As functional diversity metrics are often influenced by the number of species (Schleuter et al., 2010), we used null models to obtain an unbiased comparison between climbing mechanisms, that is, to control for the difference in number of species between active and passive climbing groups. For these null models, we randomly sampled 999 times with the replacement of a minimum common number

of species ( $n=100$ ) from each climbing mechanism. Each time, we calculated the richness, evenness and dispersion. Furthermore, we tested whether the functional diversity metrics per group were higher (indicating species functionally diverge) or lower (indicating species functionally converge) than expected by chance. To do this, we estimated richness, evenness and dispersion as before, but for a null group consisting of 100 species randomly selected from the pool, including both climbing mechanisms. Consequently, a climbing mechanism with a higher or lower value than the null group suggested functional divergence or convergence, respectively. For comparing the functional diversity metrics between climbing mechanisms (Figure 4a), we computed mean values and 95% confidence intervals. This approach allowed us to gain insights into the differences in the functional diversity patterns between the climbing mechanisms.

We assessed the functional contribution and originality of species from each climbing mechanism to the trait space formed by all liana species. Contribution measures how each species contributes to the total volume of the trait space (hypervolume). We used this metric to understand which group, active or passive climbing, has a higher functional contribution to the liana's trait space (total pool of species— $n=702$ ). Originality measures the distance between one species and a stochastic sample of species, with high values of originality indicating unique trait combinations relative to trait space (hypervolume). We used this metric to assess whether active or passive climbing has unique trait combinations relative to the liana's trait space. Both metrics, contribution and originality, enable us to understand the position of each group, active and passive climbing, in relation to the total trait space of lianas. We used a *t*-test with a significance level of  $p < 0.05$  to assess the statistical significance of the functional contribution and originality of each climbing mechanism group (Figure 3b,c) to the lianas trait space.

## 2.6 | Environmental variable predictors

We used generalized linear mixed models (GLMMs) with a binomial error term to determine the influence of environmental predictor variables on the richness of each climbing mechanism, while simultaneously controlling for phylogenetic nonindependence within each region. We included as predictors contemporary climate, past climate and vegetation structure as described above as fixed effects, and biogeographical realms (Olson et al., 2001) as a random effect to account for large-scale geographic variation. Relative proportions of climbing mechanisms were included as composite response variables (number of species in climbing mechanism  $x$ , number of species in both mechanisms combined). To facilitate the interpretation, all predictor variables were mean centred and scaled to 1 standard deviation. Furthermore, we  $\log_{10}(x+1)$  transformed mean annual precipitation, temperature seasonality, past climate temperature anomaly and precipitation anomaly to reduce skewness.

To test for issues of spatial autocorrelation and overdispersion, which lead to inflated type 1 errors (Bolker et al., 2009; Dormann

et al., 2007), we ran nonspatial GLMMs as described above and evaluated the Moran's  $I$  coefficient on our model residuals. The results indicated only low-to-moderate spatial dependency, with Moran's  $I$  values ( $I=0.11$ ,  $p < 0.05$ ) for active climbing and no spatial dependency for passive climbing ( $I=-0.001$ ,  $p > 0.6$ ). Therefore, we decided not to run spatial models. Finally, we calculated the relative importance of contemporary climate, paleoclimate, vegetation structure and phylogeny on the contribution of the richness of each climbing mechanism to global biodiversity patterns of liana species richness. All statistical analyses and maps were made in R v.4.2.1 with major input from the packages LME4 (Bates et al., 2015), JTOOLS (Long, 2022), MUMIN (Bartón, 2023), V.PHYLOMAKER2 (Jin & Qian, 2022), PHYTOOLS (Revell, 2012), PHYLOREGION (Daru et al., 2020) and GGLOT2 (Wickham & Chang, 2016).

## 3 | RESULTS

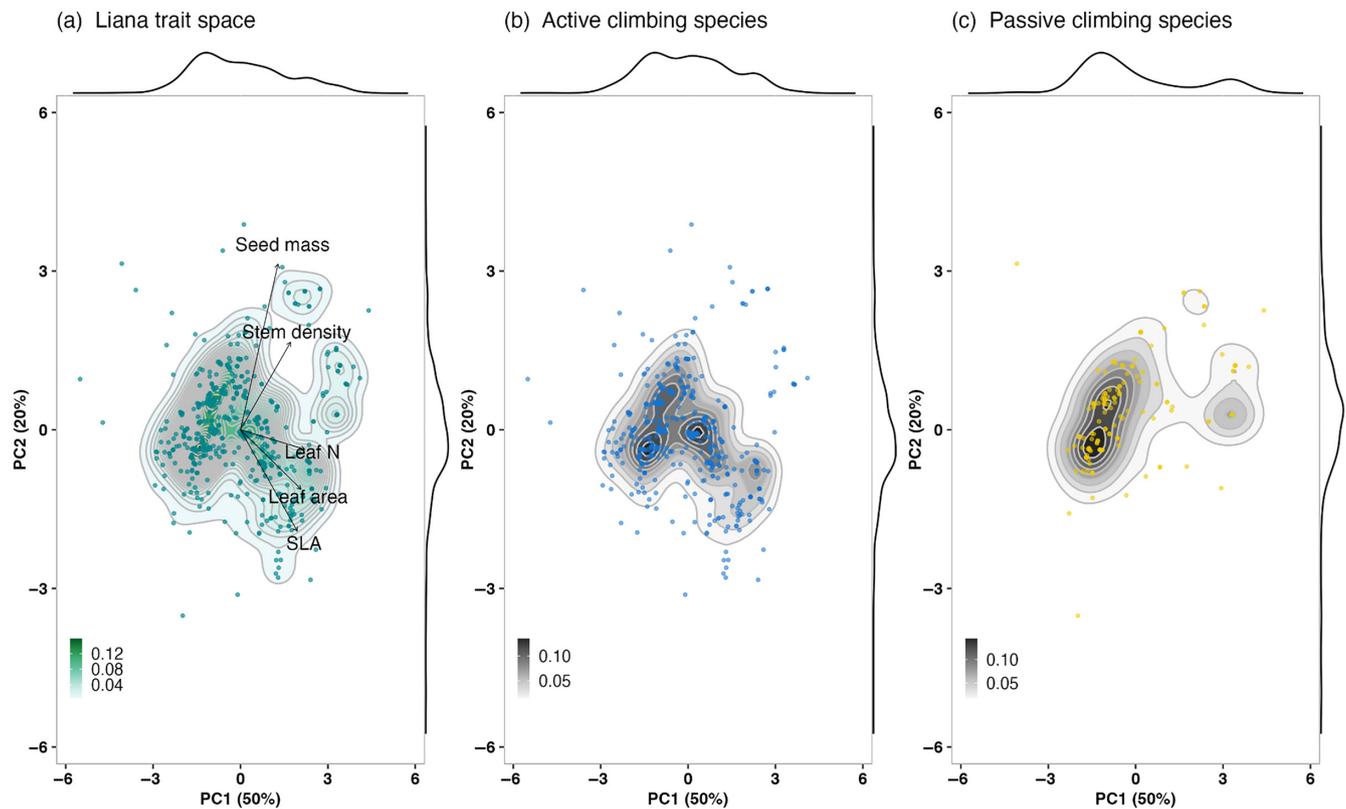
### 3.1 | Functional diversity metrics

We analysed the relationship of five functional traits (Figure 2a) for two groups of climbing mechanisms (Figure 2b,c). We found that the locations of both active and passive climbing species are highly aggregated towards the centre of lianas trait space. The active climbing trait space (Figure 2b) however encompasses a large range of trait combinations. This trait space includes plants varying in leaf economic spectrum traits (ranging from 5.56 to 93.8 mm<sup>2</sup>.mg for SLA and 1.73 to 46.5% for leaf nitrogen content). Species from this group also include plants ranging from light to heavy seeds (2.72 to 8272 mg seed mass) and from small to large leaves (0.02 to 590 cm<sup>2</sup> leaf size). The passive climbing trait space (Figure 2c) also showed a large range of trait combinations but was nevertheless restricted to lower SLA values (ranging from 9.09 to 38.2 mm<sup>2</sup>.mg) and seed mass (ranging from 0.01 to 980 mg) but included a wide range of stem-specific density (ranging from 0.3 to 1.3 g cm<sup>-3</sup>). Considering all liana species, only seed mass and stem-specific density showed a strong phylogenetic signal ( $\lambda > 0.8$ ).

Functional richness (Figure 3c) and functional evenness (Figure 3b) were significantly higher and functional dispersion (Figure 3b) was lower for species with active climbing compared with species with passive climbing. The functional contribution of active and passive climbing species (Figure 3d) did not differ, which indicates that neither group significantly increases the lianas trait space. By contrast, we found that originality was significantly higher for passive climbing species (Figure 3e; originality for active species = 1.46 and originality for passive species = 1.54).

### 3.2 | Environmental variable predictors

We found strong differences in the contribution of different climbing mechanisms to the global biodiversity patterns of lianas (Figure 4). Active climbing species consistently accounted for



**FIGURE 2** Liana trait space (a) and its dissection into two species groups (b–c) illustrating the functional diversity of species with active and passive climbing mechanisms. Projections are of the two dimensions of variation from the PC analysis (trait data are log transformed and scaled) of five functional traits. Contours are built using the 2D kernel density estimation. Gradient legends (bottom-left side) correspond to the proportion of data contained in a contour break. The density distributions of the first and second dimensions of trait spaces are displayed on the upper and right side of the trait spaces. Traits included: individual leaf area (LA), specific leaf area (SLA), foliar nitrogen content per mass ( $N_{\text{mass}}$ ), stem-specific density (WD) and seed mass (SM). Climbing mechanisms of active climbing lianas include tendrils and twiners; and those of passive climbing lianas include hooks, scramblers and roots. Note that compared with liana trait space, active climbing is aggregated towards the leaf economics spectrum, while passive climbing is aggregated towards the size spectrum.

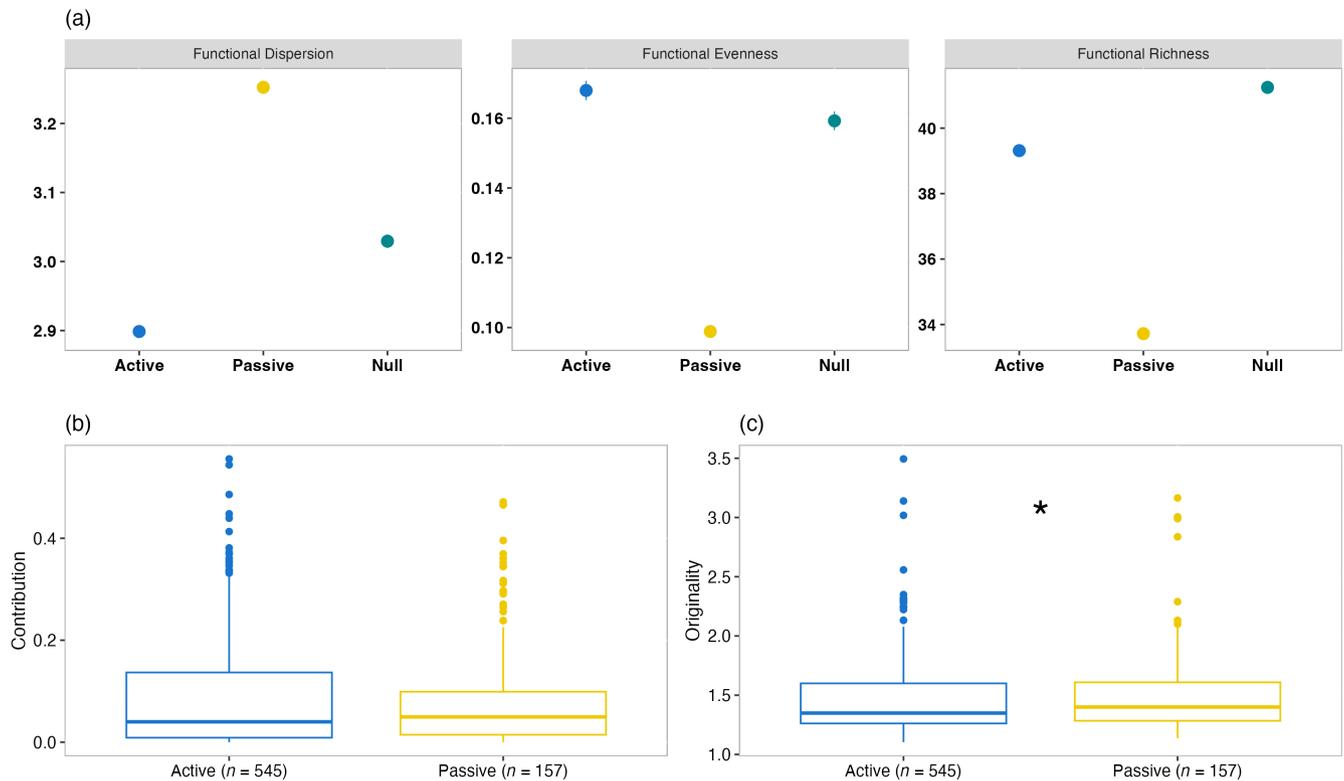
most of the plant diversity across different botanical continents (Figure 4b). Proportionally, the active climbing contribution to plant diversity was higher in Southern America than in Africa and Asia (Figure 4a).

Our models revealed a clear variation in climbing mechanism richness to gradients of contemporary climate (temperature seasonality and precipitation) and past climate (precipitation anomaly). Active climbing was positively related to precipitation (Est. = 0.20,  $p \leq 0.05$ ) and seasonality (Est. = 0.17,  $p \leq 0.05$ ), and negatively to precipitation anomaly (Est. = -0.13,  $p \leq 0.01$ ). Instead, passive climbing richness was negatively related to seasonality (Est. = -0.12,  $p \leq 0.05$ ) and positively related to precipitation anomaly (Est. = 0.10,  $p \leq 0.05$ ). The richness of both active and passive climbing species was driven by phylogeny (active climbing—Est. = -0.20,  $p \leq 0.001$ ; passive climbing—Est. = -0.28,  $p \leq 0.001$ ) (Table S4). Finally, our variable importance analysis revealed phylogeny to be the best predictor of active and passive climbing species, explaining around 44% and 57% respectively. The contemporary climate accounted for 31% of the total variance explained by our variable importance analysis for active climbing and 27% for passive climbing. Paleoclimate accounted

for 24% and 14% of the total variance explained for active and passive climbing, respectively. Remarkably, vegetation structure was a weak predictor of climbing mechanism representation, accounting only for 1% of active climbing and 0.2% of passive climbing.

## 4 | DISCUSSION

We provide compelling evidence that the type of climbing mechanism is a central trait to understand the functional and taxonomic diversity of lianas. We found a marked difference in functional diversity metrics between active and passive climbing species. Our results agree in part with our expectation that support dependency is a stronger filter for active climbing. Notably, the species in this group showed functional convergence towards similar trait combinations, as indicated by their lower richness, dispersion and originality. In addition, we found significant differences in the responses to environmental conditions between active and passive climbing mechanisms. These responses were mostly explained by phylogeny (44%–57%), contemporary climate (27%–30%), paleoclimate (14%–24%) and



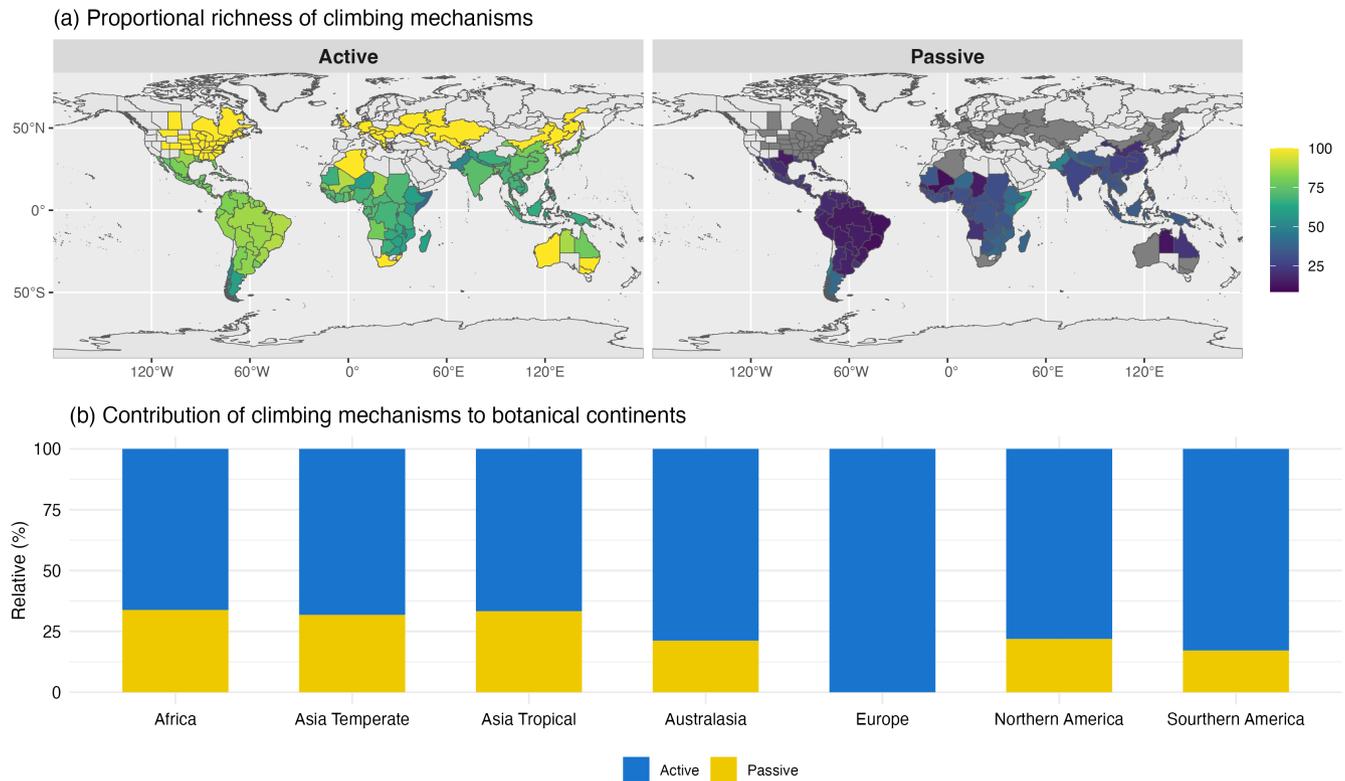
**FIGURE 3** Contribution of climbing mechanism to the functional diversity of lianas. Species groups are shown in different colours, that is in blue for active species, yellow for passive species and green for null model results (that is null) created by randomly selecting species from the liana species pool (see Methods). (a) functional richness (left), functional evenness (middle) and functional dispersion (right) were calculated using  $n$ -dimensional hypervolumes while controlling for the number of species for the two groups of climbing mechanisms ( $n=100$  species randomly sampled with replacement 999 times; see Methods). Dots and error bars correspond to the mean values and 95% confidence intervals, respectively, based on null models. Box plots with mean and 95% confidence intervals, (b) functional contribution and (c) functional originality, between species with active and passive climbing mechanisms. The asterisk in (c) refers to significant differences between active and passive species ( $t$ -test;  $p < 0.05$ ).

vegetation structure (<2%). Our results provide support for the idea that a two-group climbing mechanism classification of lianas can account for significant variation in the functional and taxonomic diversity of lianas at the global scale.

#### 4.1 | Functional diversity of lianas differs by climbing mechanisms

Most of the variability in plant aboveground traits can be summarized by two axes: one reflecting the size of the plant and the other representing the leaf economics spectrum (Diaz et al., 2016; Laughlin et al., 2020; Sterck et al., 2011; Wright et al., 2004). Our results confirm the importance of these two axes, which combined explained 70% of the variation in the lianas trait space (Figure 2a). However, active climbing species are aggregated towards the leaf economic spectrum (Figure 2b), while the passive climbing species are more aggregated towards the size spectrum (Figure 2c). The higher functional richness of active climbers implies broader niche exploration than passive climbers, probably because active climbers can both grow in shaded understory conditions as well exposed high light conditions (Medina-Vega et al., 2021), whereas passive

climbers are more restricted to the shaded understory. Indeed, lianas' growth and potential acclimation, inside and across forests, depend on their climbing mechanism (DeWalt et al., 2000; Putz, 1984; Putz & Holbrook, 1991). However, in contrast to trees, the rate of stem elongation, more than the investment in diameter increase, plays a central role in the liana's ability to find a suitable support. For instance, there is evidence that lianas exhibit higher rates of shoot elongation compared with trees (Bai et al., 2020; Ichihashi & Tatenno, 2015; Roeder et al., 2012; Schnitzer, 2005), and that active species have higher rates of shoot elongation compared with passive species (Teramura et al., 1991). The functional trait differences we found between the active and passive species support the idea of active climbing species having faster growth towards fully exposed conditions in the upper forest canopy and benefiting from a more acquisitive strategy. However, the low number of different functional traits measured for the same species represents a limitation for macroecological studies of lianas (see Willson et al., 2022, Figure S3). We partially overcame this limitation by using a trait imputation approach. Therefore, we emphasize that more data on multiple functional traits for the same individuals of liana species are urgently needed to enable more robust tests of the a priori climbing mechanism classification we used.



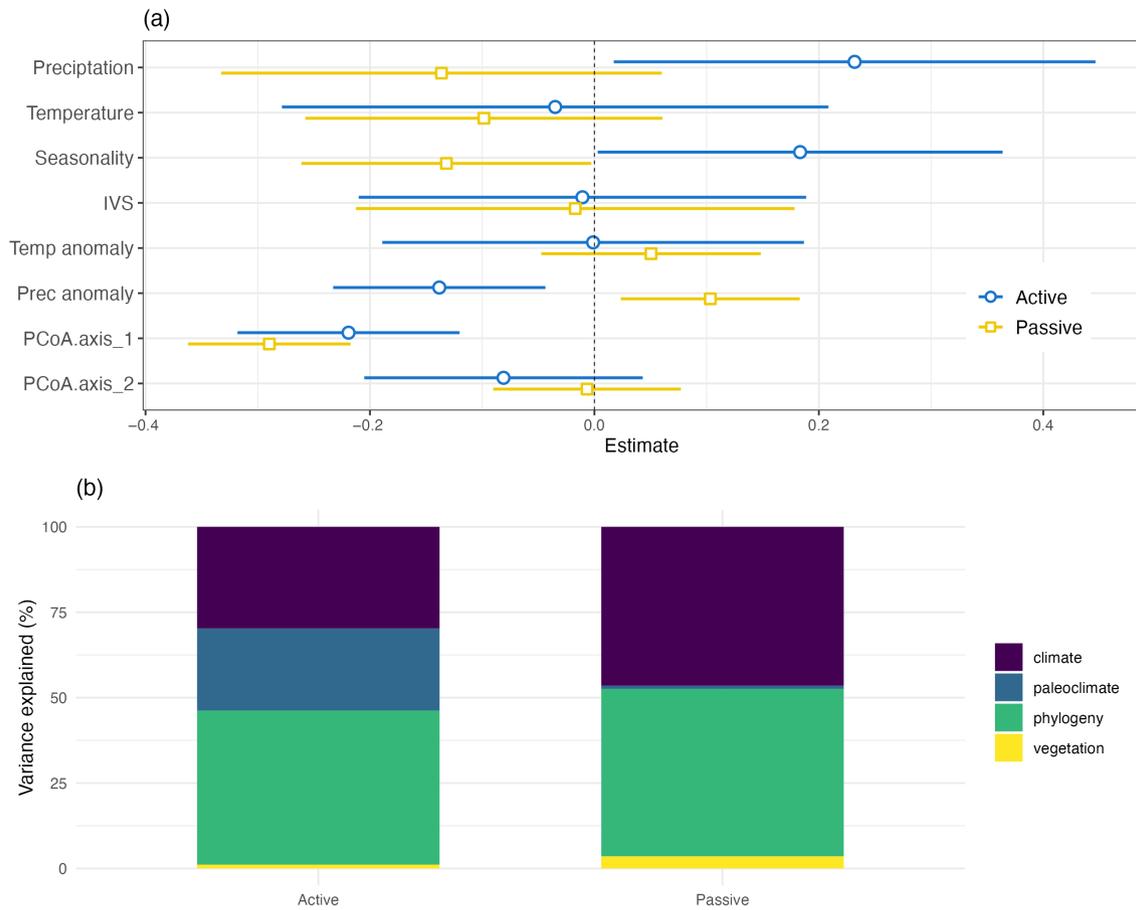
**FIGURE 4** Global patterns of liana species richness by climbing mechanisms (a), quantified here as the proportion of the respective climbing mechanisms (active and passive) relative to the total number of lianas for each botanical country. Proportional contribution of liana species by climbing mechanisms to (b) botanical continents.

Functional richness, evenness and dispersion at the group level, and contribution and originality at the species level, are complementary facets that describe the magnitude of distinct dimensions (or estimations) of diversity (Mouchet et al., 2010). Our results show that support dependency is likely to be a stronger filter for certain traits in active than passive climbing lianas. For instance, active species showed lower richness and dispersion (compared with the null model) and lower originality, indicating functional convergence. This is likely to reflect the strong filter of external support for active species to grow successfully. Instead, active species showed higher evenness (compared with the null model), indicating that certain combinations of traits are not more common than others. This suggests that active species are more likely to have a range of different trait combinations to explore the vertical gradient from the low-light forest floor to the high-light canopy. Indeed, active climbing species tend to reach the canopy and spread over different host crowns, developing a more aggressive strategy in terms of space occupation compared with passive climbing species (Ichihashi & Tateno, 2015; Isnard & Silk, 2009; Medina-Vega et al., 2021; Rowe & Speck, 2004). The lower functional convergence of passive climbing lianas may be due to a combination of evolutionary and ecological forces. For instance, the simple scrambling mechanism, which requires little developmental and morphological changes, is widely distributed in the phylogeny of angiosperms, indicating that this might be one of the easiest climbing mechanisms to evolve (Sperotto et al., 2020). Instead, species with a root-climber mechanism appear

to be concentrated in the wettest areas—reflecting ecological filtering (Durigon et al., 2013; Sperotto et al., 2023). These results support the hypothesis that active climbers occupy a wider range of niches than passive climbers, which tend to be restricted to the shaded forest understory (Carter et al., 1988; Dias et al., 2019; Ichihashi & Tateno, 2011; Wyka et al., 2013). In summary, our results indicate that not only the type of climbing mechanism but also the presence of other traits, and the interaction between them and the environment determine the ecological range of lianas (Figure 5).

## 4.2 | Environmental variable predictors and distribution of climbing mechanisms

We found consistent differences in the relative contributions of active and passive climbing to the global gradient of lianas diversity. Overall, there are more active climbing species than passive climbing ones across all botanical continents. However, passive climbing species are proportionally more speciose in Africa and Asia Tropical. Surprisingly, these biogeographical differences in relative richness are not driven by forest structure. For instance, we found our Index of Vegetation Structure (IVS—canopy height multiplied by tree density) as the weakest, and not significant, predictor of both active and passive climbing richness. Our results contrast with a recent study showing that across the Neotropics, the liana species richness from the tribe Bignoniae, which in general has a type of active climbing



**FIGURE 5** Coefficient plot showing the standardized effects of mean annual precipitation (precipitation, mm), mean annual temperature (temperature, °C), temperature seasonality (seasonality, coefficient of variation of temperature), Index of Vegetation Structure (IVS, trees per m), past climate anomaly of temperature (temp anomaly, mm yr<sup>-1</sup>) and precipitation (prec anomaly, mm yr<sup>-1</sup>), and phylogeny (principal coordinate analysis (PCoA) 1–2, as components from a principal coordinates analysis) on the proportional representation of liana species with active and passive climbing mechanisms (a). Variable importance (b) plot depicts the combined importance of contemporary climate (climate), paleoclimate, forest structure (vegetation) and phylogeny on climbing mechanisms' contribution to patterns of liana species diversity. Detailed model results used to create this figure can be found in Support Information Extended Data 1.

mechanism (tendrils climbers), was positively related to canopy height (Meyer et al., 2020). There are two possible explanations for these different results. First, our study analysed a wide group of liana species and not only a specific clade as in Meyer et al. (2020). Second, it is possible that vegetation structure, as measured by the IVS, did not sufficiently capture the availability of support for the distribution of climbing mechanisms. Alternatively, the support-dependence of each type of climbing mechanism to the vegetation might be better captured with plot-scale data considering the density of trees but also their individual height and diameter. Further studies using plot-level data and looking at a continuum from forests to open areas may provide an important way to assess how vegetation structure determines climbing mechanisms distribution.

Consistent with our second hypothesis, some of the main climate predictors of species distribution are significantly associated with active and passive climbing mechanisms. While temperature seasonality was positively associated with active climbing, it was negatively associated with passive climbing. The positive relationship between active climbing richness with temperature may reflect the higher

potential of acclimation and phenotypic plasticity of active climbers. For instance, (Carter et al., 1988) analysed the photosynthetic acclimation of lianas and found that passive species displayed greater physiological acclimation to low-light environments, while active species were found to have the broadest physiological plasticity to high-light environments. In general, our results support the idea of niche partitioning among lianas to climatic gradients when considering their climbing mechanisms. Indeed, a previous study showed that root climbers (a passive climbing mechanism) occurrence reduces towards increasing temperature in tropical sites (Durigon et al., 2013), but our results show that climate filtering also explains distribution differences between active versus passive climbers.

Past climate stability, in our approach measured as precipitation anomaly, left a strong legacy effect on both active and passive climbing species. This result implies that the Quaternary climate plays an important role in shaping present-day patterns of lianas distribution. Active climbing species were associated with climates that have remained relatively stable through time (negative association with precipitation anomaly). Passive climbing species, on the contrary, were

positively associated with precipitation anomaly. These results imply that major climate dynamics at long time scales may contribute to the current abundance of active and passive climbing species across the globe. Indeed, shifts in global rainfall patterns are prompting changes in the relative distribution of plant growth forms within specific ecosystems (Zhang et al., 2019). Our results also highlight that active and passive climbing might have different niche lability. Even though we did not test the effect of niche conservatism, there is evidence of niche conservatism of growth form (trees, herbs, shrubs and climbers) across forest–savanna transitions in Africa (Gorel et al., 2022), for example. Future studies looking at the lability of climatic niche and climbing mechanisms would provide an interesting avenue to understand how niche conservatism structures the distribution of lianas.

We found that phylogenetic relatedness plays an even more important role than climate and paleoclimate in explaining the distribution of active and passive climbing mechanisms. The stronger effect of phylogeny on the representation of active and passive climbing species may be related to the limited number of lineages that undergo local radiations, rather than by the convergence of climbing mechanisms in regions with similar climates (Sperotto et al., 2020, 2023). For instance, when species concentrated in a given climate or region are represented by a few families, this pattern might be a consequence of shared ancestry rather than independent events of the evolution of that climbing mechanism (Sperotto et al., 2023).

Leveraging one of the world's largest botanical databases, the World Checklist of Vascular Plants (WCVP v.2.0, Govaerts et al., 2021), our study revealed significant and contrasting associations between current climate and paleoclimate with the species richness of active and passive climbing mechanisms. However, our study included information only for species occurrence but not for the number of individuals. Abundance is an important component of species diversity, and its consideration provides a more comprehensive and nuanced perspective on ecological communities (Keil & Chase, 2019), particularly for tracking the impacts of climate change and habitat loss. We suggest that future studies using abundance, from plot-level data, associated with liana climbing mechanisms could test the generality of our findings while accounting simultaneously for species richness and abundance. Such studies will provide the opportunity to disentangle the main drivers of richness and abundance of lianas and their response to climate change.

## 5 | CONCLUSIONS

This study highlights the importance of climbing mechanisms to understand global patterns in functional diversity and distribution of lianas. The evolution of different climbing mechanisms and its implication for the life history of lianas is understudied, but essential to link species response to climate change. Here, we showed that passive climbing lianas differed in functional diversity and their richness–environment relationship patterns compared with active climbing lianas. Overall, filtering related to support dependency

and forest vertical heterogeneity contribute to the functional convergence and divergence between active and passive climbing lianas. Additionally, the legacy of the Quaternary climate reflects a strong imprint in active than passive climbing lianas, showing the importance of past climate to explain the current pattern of lianas distribution.

The increase in liana abundance and biomass in recent decades across the tropics is not uniform: increasing in the Neotropics but rather stable in the Afrotropic and mixed in Indo-Malay (Schnitzer, 2018; Schnitzer & Bongers, 2011). We conclude that life history (climbing mechanisms) and functional traits have to be taken into account to understand such different lianas responses across continents, and their cascading effects across ecosystems. The expansion and accessibility of global data (such as BIEN and TRY in recent years), creates a huge opportunity to further understand such potential mechanisms underlying the species and functional diversity of liana communities and their responses to climate change across tropical forests worldwide.

## AUTHOR CONTRIBUTIONS

Arildo S. Dias conceived the ideas, performed the meta-analysis and statistical modelling and analysed the output data. Rafael S. Oliveira, Fernando R. Martins, Frans Bongers, Niels P. R. Anten and Frank J. Sterck contributed to the interpretation of the results. Arildo S. Dias wrote the first draft of the manuscript. All authors contributed to the revisions.

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## CONFLICT OF INTEREST STATEMENT

We declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

This paper does not have new data to be archived. All data used in the manuscript are openly available or archived in the BIEN and TRY databases and the associated supplementary material. Code and data to reproduce the main analyses are archived at Zenodo: [zenodo.org/records/10827342](https://zenodo.org/records/10827342) and mirrored at the GitHub repository: <https://github.com/arildodias/lianas-climbing-mechanisms-trait-data>

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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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