Climbing Strategies: A Key to Understanding Liana Ecology in Tropical Forests

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Abstract: **Lianas are a central component of tropical forests, yet the relationship between their climbing mechanisms and the functional and taxonomic diversity across the tropics remains poorly understood. In this study, we tested two main hypotheses: (a) that the functional diversity of lianas varies with climbing mechanism, distinguishing between active (e.g., twining, tendrils) and passive (e.g., scramblers, hookers) climbers, and (b) that the association between taxonomic diversity and factors such as contemporary climate, forest structure, and phylogeny differs between climbing mechanisms. By analyzing functional traits and taxonomic diversity across a broad range of tropical environments, the study aims to clarify the ecological and evolutionary drivers shaping liana diversity. Our findings are expected to provide novel insights into the role of climbing strategies in the adaptive success of lianas and their contribution to forest dynamics under varying environmental conditions. The study highlights significant differences in functional diversity specifically in terms of richness, dispersion, evenness, and originality between active and passive climbing species. These differences likely reflect distinct ecological strategies for resource use, stress tolerance, and dispersal. By integrating taxonomic and functional diversity metrics with data on climbing mechanisms, it provides more comprehensive understanding of the ecological roles of lianas and their varying responses to environmental factors, including climate change. This approach offers deeper insights into how lianas may adapt to or be affected by shifting climatic conditions in tropical forests.**

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

I. INTRODUCTION

One of the most significant changes in tropical forests over the past three decades is the marked increase in liana abundance and biomass (Schnitzer, 2018; Schnitzer & Bongers, 2011; Yorke et al., 2013). Lianas, which are non-self-supporting woody climbers, invest more in leaf mass relative to cross-sectional stem area than trees. As a result, they rely on surrounding vegetation for support to access the forest canopy (Gerwing et al., 2006; Schnitzer & Bongers, 2002). Studies indicate a rise in liana abundance and biomass in Neotropical forests (see Schnitzer & Bongers, 2011). In contrast, studies in African tropical forests have not observed a similar increase in liana populations (Bongers et al., 2020; Schnitzer, 2018).

This discrepancy may stem from variations in species biogeographical distribution and functional traits. Furthermore, liana abundance and biomass at larger spatial scales may be influenced by climate seasonality (Schnitzer, 2005), soil conditions (van der Heijden & Phillips, 2008), and disturbance dynamics (Schnitzer, 2018). Despite these insights, the underlying reasons for the differences in functional and

taxonomic diversity of lianas across tropical forests and the potential role of climbing mechanisms in mediating these differences remain poorly understood. Lianas have garnered significant interest from botanists due to their unique climbing mechanisms and growth strategies (Darwin, 1875; Isnard & Silk, 2009). Their vertical growth is supported by a diverse array of attachment systems (Isnard & Silk, 2009; Rowe & Speck, 2004; Putz, 1984; Speck & Burgert, 2011). The type of climbing mechanism directly influences the maximum distance a liana can span between supports and determines its climbing success, which is also contingent upon the maximum stem diameter of the supports that lianas can colonize (Isnard & Silk, 2009; Putz & Holbrook, 1991; Rowe & Speck, 2004). In his seminal work The Climbing Movement of Plants (1875), Darwin characterized hook climbers as having the least efficient climbing mechanism, followed by root climbers, while identifying twining and tendril climbers as the most efficient. However, classifications of climbing mechanisms in lianas vary widely in the literature, with some studies proposing as few as three categories (Vaughn & Bowling, 2011) and others presenting up to ten (Bongers et al., 2005), as recently reviewed by Sperotto et al. (2020).

In this study, adopting the classification framework proposed by Sperotto et al. (2020), which delineates two primary categories: active climbing species, characterized by highly specialized attachment systems that enable them to span multiple host trees, and passive climbing species, which lack these specialized systems and are typically restricted to climbing one or a few host trees. This framework allows for a clearer understanding of the ecological implications of liana climbing mechanisms and their adaptive strategies in tropical forests. Active climbing lianas are plants displaying a support-searching behavior such as circumnutation and include species with tendril and twiner climbing mechanisms. Rather, lianas that passively climb simply grow over or rest on their supports without actively seeking out new ones; this category includes species that have hooks and scrambles and adhesive roots (hereafter roots) as a climbing mechanism.

Ecological niche differentiation is evident among liana species that employ different climbing mechanisms, as demonstrated in previous studies (Kusumoto et al., 2013; Putz, 1984). For example, liana species that utilize adventitious roots for passive climbing typically inhabit the inner, less illuminated regions of the tropical forest canopy (Kusumoto et al., 2013) and exhibit the lowest photosynthetic rates when compared to their temperate counterparts (Carter et al., 1988). In contrast, tropical lianas that employ tendrils for active climbing generally have shorter foliage retention durations than passive climbing lianas

in the same environment (Hegarty, 1990). These tendril climbers also tend to prefer sites with a high density of slender supporting stems, indicating a specialization for early successional habitats (DeWalt et al., 2000). Despite this evidence of ecological differentiation, the overall implications of climbing mechanisms for the functional trait diversity of lianas remain largely unexplored. Further investigation into how climbing strategies influence functional traits will enhance our understanding of liana ecology and their roles within tropical forest ecosystems.

An emerging question in the study of liana life histories is whether different types of climbing mechanisms are associated with specific trait syndromes and whether there is coordination among individual traits that reflects ecological strategies along a conservative-acquisitive continuum, such as the leaf economic spectrum. The theoretical basis for this hypothesis is grounded in the understanding that climbing mechanisms limit the maximum size of the support available for vertical growth (e.g., the maximum stem diameter to which a climbing mechanism can attach) and the light environments accessible for growth (Darwin, 1875; Putz & Holbrook, 1991; Putz, 1984). Active climbing species generally possess more flexible stems (higher modulus of elasticity) than their passive counterparts (Isnard & Silk, 2009; Rowe & Speck, 2015; Speck & Burgert, 2011). This increased flexibility may facilitate higher shoot elongation rates and improved access to high-light conditions in the upper canopy. However, within the active climbing group, tendril climbers are often limited to attaching to trees with smaller diameters compared to twining species (Putz, 1984; Putz & Chai, 1987). Consequently, in forests characterized by high rates of fragmentation or gap formation, where smaller trees dominate, tendril species tend to be more abundant (DeWalt et al., 2015; Letcher & Chazdon, 2009).

Additionally, the influence of different climbing mechanisms may vary along climate gradients. While liana abundance generally increases across the tropics, peaking in seasonally dry forests (Schnitzer, 2005), root climbers (passive climbers) are more frequently found in sites with higher precipitation levels (Durigon et al., 2013). Despite these observed patterns, the extent to which climbing mechanisms are related to trait diversity in lianas, and how environmental factors such as forest structure and climate influence the distribution patterns of climbing mechanisms, remain largely unanswered. Further research is needed to elucidate these relationships and their ecological implications for liana diversity in tropical ecosystems.

A trait-based perspective examines how ecological and evolutionary dynamics shape the trait space a multidimensional hypervolume that may lead to functional convergence or divergence (Mammola & Cardoso, 2020). Within this framework, diversity among groups can be represented by three primary dimensions: richness, dispersion, and evenness, which together reflect variations in the trait space (Mammola & Cardoso, 2020; Mammola et al., 2021). At the species level, a species' position within the trait space can indicate its uniqueness or originality and its contribution to overall diversity.

Focusing on lianas, their dependency on support for vertical growth acts as a significant filter that may restrict the trait space,

potentially favoring functional convergence. For instance, the presence of G-fibers, which are specialized wood cells facilitating stem movement, is common among active climbing species but absent in passive climbing species (Chery et al., 2022). In contrast, the vertical heterogeneity of the forest, from the floor to the canopy, presents ecological opportunities that allow for the development of diverse trait combinations, thereby facilitating functional divergence. Despite these insights, the extent to which climbing mechanisms influence functional diversity encompassing richness, dispersion, and evenness in lianas remains poorly understood. This raises an important question regarding the degree of similarity or distinction among lianas based on their climbing strategies and their implications for ecological interactions and forest dynamics. Further research is necessary to explore these relationships and clarify how climbing mechanisms shape the functional diversity of lianas in tropical ecosystems.
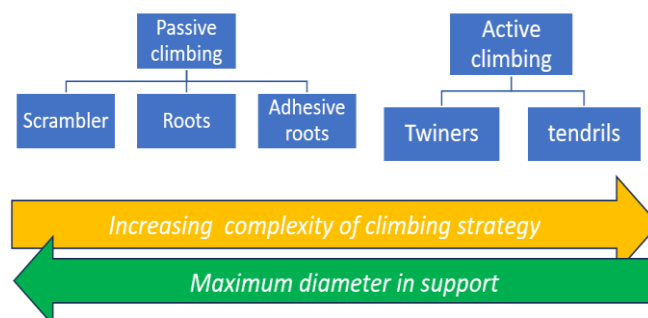

Figure 1: Ecological niche differentiation is evident among liana species

This study evaluates the importance of passive versus active climbing mechanisms concerning global liana species distributions and multiple aspects of functional diversity at both the group level (functional richness, dispersion, and evenness) and the species level (contribution and originality) (Mammola & Cardoso, 2020). To accomplish this, by synthesising data on lianas, emphasising the principal functional features that define plant morphology and functionality. Liana species were categorised into active and passive climbing classifications, as per the climbing mechanism classification established by Sperotto et al., 2020. Furthermore, incorporating the climbing techniques of liana species with an extensive global checklist that includes over 295,000 vascular plant species distributions (Govaerts et al., 2021). This integration enabled us to assess the significance of active and passive climbing mechanisms in influencing liana taxonomic diversity patterns across various biogeographical regions and to investigate their relationships with current and historical climate conditions, vegetation structure, and phylogeny. The subsequent hypotheses were evaluated:

1. The study propose that lianas are strongly filtered ecologically by support dependency, which is the requirement for an external support (such as a tree or shrub) in order to grow vertically towards the canopy. In that case, we assume that active climbing, which has a stronger support dependency evidenced by its specialized climbing structures, shows better functional variety at the group level (richness, divergence and regularity) and the species level (contribution and originality) than passive climbing.

2. The kind of climbing mechanism used can influence one's odds of success in a given setting. As a result, by anticipating the current climate, the paleoclimate, and vegetation,

structure and species evolutionary relationships, or phylogeny, to have distinct effects on the distribution of climbing species that are active and passive. Additionally, given that lianas often consist of a limited number of species-rich plant families, Location is expected to play a major role in the phylogeny of both passive and active climbing

II. MATERIALS AND METHODS

Functional traits and climbing strategies

Developing a trait dataset utilized trait data from the BIEN Database and peer-reviewed studies (R package 'BIEN' version 4.1.1, Maitner et al., 2018). Among 704 climbing and liana species, 545 exhibited characteristics indicative of active climbing, whereas 157 had traits associated with passive climbing. Utilizing species-level data, it is confined the analysis to the following functional traits: wood density (WD), individual leaf area (LA), specific leaf area (SLA), foliar nitrogen content per mass (Nmass), and seed mass (SM). It focused on woody climbing angiosperms (lianas).

Using the liana concept as put forward earlier (Gerwing et al.2006) is combined i.e. "climbing plants with xylem tissues that produce true wood" originating from a vascular cambium and that begin life on the ground but, as they develop, become unable to sustain themselves and must instead rely on outside physical assistance to reach the canopy. As a result, it excluded taxa that were categorized as "hemi epiphyte." But it is observed the woodiness criterion will leave out several dicotyledon genera, such Passiflora, despite having perennial fibrous stems, Ipomoea and numerous Cucurbitaceae are prevalent and significant in many liana inventories (Gentry, 1991; Gerwing et al., 2006). Therefore, in addition to species from the family Cucurbitaceae, it also included species from the genera Passiflora and Ipomoea in the analysis. Species showing different classifications for their climbing strategies were excluded to minimize uncertainties. After a thorough review of the literature, it is classified each liana species based on the sort of climbing mechanism that they used.

To learn more about the kind of climbing mechanism, this study looked through databases and online resources (such as virtual herbaria and online floras). It classified liana ascending processes in the wake of (Sperotto et al. 2020) and concentrated on contrasting the active and passive climbing strategies employed by lianas. It restricted the scope of search to studies that reported characteristics of adult plants growing in natural environments, and only considered species that were recognized to the binomial level. Data from seedlings, saplings, and plants growing in experimental settings were therefore excluded from the analysis. The study compiled data from 42 research totaling 702 species of climbers and lianas, including information each species' at least one of the aforementioned features.

As recommended by other research (Johnson et al., 2020; Joswig et al., 2023; Penone et al., 2014), This study employed phylogenetic trait imputation to get around the problem of species with missing data for the traits dataset. Using the R package V.PHYLOMAKER2 (Jin & Qian, 2022), It constructed a phylogenetic tree and imputed trait values using the phylogenetic data. The missForest function in the MissForest R package, a random forest technique, was utilized to accomplish the imputation of missing trait data (Stekhoven & Bühlmann, 2012). Using the out-of-bag error method to evaluate the algorithm's predicted accuracy. This method involved contrasting a different methodology that predicts trait values without taking phylogenetic information into account with the random forest approach, which took into account phylogenetic relationships across species. For the majority of features, the results showed that the phylogenetically informed imputation performed as well as or better than the alternative method. Lastly, using the phylosig function in the R package phytools (Revell, 2012) to estimate the phylogenetic signal for each trait with Pagel's λ, taking into account that closely related species typically have comparable trait values. By employing the out-of-bag method to evaluate the algorithm's predicted accuracy. error-prone method. This method involved contrasting the random forest.

Since closely related species typically exhibit comparable trait values, using the phylosig function in the R package phytools to estimate the phylogenetic signal for each trait using Pagel's λ(Revell,2012). Constructing a phylogenetic tree that included every species of liana. To accomplish this, the expanded phylogeny by (Smith and Brown 2018), available in the R package V.PHYLOMAKER2 (Jin & Yian, 2022), was utilized. Before trait imputation, the phylogenetic signal was estimated.

Species richness

The study employed the RBG Kew's World Checklist of Vascular Plants (henceforth referred to as "WCVP"; Govaerts et al., 2021) to maintain only approved names in the database and to standardize the taxonomy by eliminating names that are synonyms, illegitimate, or unresolved. The final database includes 702 species, each of which has a score based on the kind of climbing mechanism. This final database was used for further analysis. The World Geographical Scheme for Recording Plant Distributions (WGSRPD, Brummitt et al., 2001) uses the level of "Botanical Country" to record species distributions from the WCVP.

The number of species within the level of "Botanical Country" (henceforth referred to as region) is calculated the absolute species richness for liana species and for each climbing mechanism individually. The entire wealth of the proportional percentage of each climbing method within each location was determined using lianas. More precisely, "climbing mechanism richness" is the total of all liana species of a certain climbing mechanism within a territory, and "total liana richness" is the sum of all liana species within a region.

Environmental predictor variables

Because lianas depend on readily accessible trees for climbing, utilizing an index to represent forest structure as the result of multiplying canopy height by tree density. Extracted the canopy height at 1km^2 for each region. tree density at 1 km^2 resolution from (Crowther et al. 2015) and resolution from (Simard et al. 2011), and multiplied both values. To evaluate the relationship between climbing mechanisms and the current climate, three bioclimatic indicators with a precision of 30 arc-seconds were taken from CHELSA v.2.1 (Karger et al., 2017).

The following bioclimatic factors are significant in identifying patterns of plant diversity: mean annual temperature (°C), mean annual precipitation (mm), and temperature seasonality (coefficient of variation of mean annual temperature) (Cai et al., 2023; Kreft & Jetz, 2007; Scheiner & Rey-Benayas, 1994). By computing the difference in mean annual temperature and precipitation between the current environment and the Last Maximum Glacial (LMG), the possible influence of historical climate on each climbing mechanism was examined. The temperature and precipitation anomaly, which is the difference between the mean annual temperature and precipitation at the LMG and the present, is computed for every grid cell and then aggregated to the level of the entire country. Temperature and precipitation LMG data were taken at a resolution of 30 arc-seconds from the PaleoClim database (Brown et al., 2018).

Phylogenetic predator variables

The study computed region-level phylogenetic eigenvectors as additional predictor variables in the models to separate the ecological and evolutionary effects to the patterns of climbing mechanism richness. First, using the extended (Smith and Brown 2018) phylogeny, which was implemented in the R package V.PHYLOMAKER2 (Jin & Qian, 2022), building the phylogenetic tree. In scenario 3, it created a phylogenetic tree hypothesis using the phylo.maker tool (Jin & Qian, 2022). Despite the fact that scenario 3 includes polytomies for missing species, other research has shown how reliable this method is for extensive biogeographical assessments (Cai et al., 2023; Qian & Jin, 2016, 2021).

Because the Simpson index is insensitive to changes in species richness across sites, I used it to assess phylogenetic turnover (Phyloobs) between regions for each climbing method individually in the second stage (Baselga, 2010). Nonetheless, the species compositional turnover impacts the phylogenetic turnover in a manner akin to the robust impact of species richness on phylogenetic richness. In order to address this problem, by measuring the standardized effect size of Phyloses, or phylogenetic turnover, for every climbing mechanism, taking into consideration regional differences in compositional turnover.

Using the R PHYLOREGION package, computing the Phyloses (Daru et al., 2020). By rearranging the tip names in the evolutionary tree 1000 times for each climbing mechanism independently, I produced several null assemblages and able to determine the standard deviation (PhyloSD) and mean null phylogenetic turnover (Phylomean_null) using this process. Next, computing Phyloses = (Phylomean_null – Phyloobs)/PhyloSD. In order to generate phylogenetic eigenvectors at the regional level and carried out a principal coordinates analysis (PcoA) on the resulting Phyloses distance matrix in the third phase.

By capturing the entire range of variance in phylogenetic makeup between regions in this way. These eigenvectors served as our model's predictor variables. It evaluates how the phylogenetic relatedness of the species across regions affects the patterns of climbing mechanism richness inside a particular region using these phylogenetic eigenvectors. The initial two PcoA axes were incorporated into the models.

Statistical analysis

Functional diversity metrics

Using the methodology of (Barajas Barbosa et al. 2023) and Mammola and (Cardoso 2020), The study assessed the contribution of active (n = 545) and passive (n = 157) climbing species to the total liana trait space in order to examine how climbing mechanisms may have affected the functional variety of lianas.

Using the log-transformed and z-transformed (centered and rescaled to unit variance) mean trait values, first ran a principal component analysis (PCA) to map trait spaces. Then carried out one PCA utilizing every species of liana and a different PCA for every type of climbing mechanism. Next, in contrast to other techniques, by employing the n-dimensional functional hypervolume approach (Blonder, 2018), which appropriately compensates for gaps in the trait space (Villéger et al., 2008). Here, the hypervolume is defined by the first three principal components obtained from the PCA. Various features of diversity, such as richness, dispersion, and evenness, can be characterized by the location of the observations (species, for example) in this multidimensional space.

The study employed the Gaussian approach, which fits the data loosely and shows less sensitivity to bandwidth change, to construct the hypervolumes. According to (Blonder 2018), these qualities are especially appropriate for functional diversity estimate. The study initially created hypervolumes using the principal components from PCAs ran for each distinct dataset in order to evaluate the overlap between the trait spaces (all liana species combined, active climbing, and passive climbing). Each unique dataset was assigned a fixed kernel bandwidth, which was determined using the estimate bandwidth function in the Hypervolume R package (Blonder, 2018). This study evaluated richness, evenness, and dispersion three aspects of functional diversity for every climbing mechanism. By estimating richness, evenness, and dispersion using the functions kernel.alpha, kernel.evenness, and kernel.dispersion from the R package BAT (Mammola & Cardoso, 2020), in that order. The hypervolume, or overall volume, of a trait space is measured by functional richness. By computing the average difference between the centroid and

species (points) randomly positioned inside the bounds of the hypervolume, functional dispersion quantifies how dispersed, or dense, a particular trait space is (Mammola & Cardoso, 2020). By computing the overlap between an observed hypervolume and a theoretical hypervolume, where traits and abundance are uniformly distributed throughout the entire trait space, functional evenness quantifies the regularity of a trait space (Mammola & Cardoso, 2020). Since the number of species has a significant impact on functional diversity metrics (Schleuter et al., 2010), by employing null models to adjust for the variation in species across active and passive climbing groups in order to achieve an objective comparison between climbing processes. By replacing a minimum common number of species (n = 100) from each climbing mechanism in 999 random samples for these null models. It is determined that the richness, evenness, and dispersion each time.

Furthermore, examining whether species functional divergence or convergence was suggested by elevated functional diversity metrics per group compared to what would be anticipated by chance. To do this, performing the same analyses of richness, evenness, and dispersion as previously, but for a null group of 100 species that were chosen at random from the pool and included both climbing methods. Thus, functional divergence or convergence was suggested by a climbing mechanism whose value was higher or lower than that of the null group, respectively. To compare the functional diversity metrics amongst climbing mechanisms, it is calculated 95% confidence intervals and mean values. It is learned more about the variations in the functional diversity patterns among the climbing mechanisms thanks to this method.

Evaluating the uniqueness and functional contribution of each climbing mechanism's species to the trait space that all liana species have produced. Contribution quantifies the amount that each species adds to the trait space's overall volume, or hypervolume. Using this metric, it is determining which group passive or active climbing contributes more functionally to the liana's trait space (total poll of species, n = 702). High originality ratings indicate unique trait combinations relative to trait space (hypervolume), and originality evaluates the distance between one species and a stochastic sample of species. In relation to the trait space of the liana, this metric to determine if active or passive climbing has unique trait combinations. By comprehending each group's position, active and passive climbing, in respect to the entire trait space of lianas by using both metrics contribution and originality. The statistical importance of each climbing mechanism group's functional contribution and uniqueness to the liana's trait space was evaluated using a t-test at a significance threshold of $p < 0.05$.

Environmental variable predictors

In order to account for phylogenetic non independence within each region and assess the impact of environmental predictor variables on the richness of each climbing mechanism, Binomial error term-based generalized linear mixed models (GLMMs) were employed. As a way to account

for large-scale regional variation, by incorporating biogeographical realms (Olson et al., 2001) as a random influence in addition to the fixed effects of past climate, vegetation structure, and current climate as predictors. As composite response variables, relative proportions of the climbing mechanisms (number of species in climbing mechanism x, number of species in both mechanisms combined) were included. All predictor variables were scaled to one standard deviation and mean centered in order to aid in interpretation. Furthermore, mean annual precipitation, temperature seasonality, previous climatic temperature anomaly, and precipitation anomaly were $log10(x + 1)$ transformed to decrease skewness.

Using the previously mentioned nonspatial GLMMs, it is tested for problems with spatial autocorrelation and overdispersion, which cause inflated type 1 errors (Bolker et al., 2009; Dormann et al., 2007). The Moran's I coefficient was also assessed on the model residuals. The findings showed that there was no spatial dependency for passive climbing (I = −0.001, p > 0.6) and only low-to-moderate spatial dependency for active climbing (I = 0.11, p < 0.05). As a result, spatial models were not chosen. Lastly, the relative contributions of each climbing mechanism's richness to worldwide patterns of liana species richness were computed, taking into account the current climate, paleoclimate, vegetation structure, and phylogeny. With significant assistance 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 GGPLOT2 (Wickham & Chang, 2016), all statistical analyses and maps were created using R v.4.2.1.

III. RESULTS

Functional diversity metrics

Five functional features were studied in relation to two groups of climbing mechanisms. It was discovered that the centers of the liana trait space are where the sites of both active and passive climbing species are heavily concentrated. However, a wide variety of trait combinations are included in the active climbing trait space. Plants with different leaf economic spectrum features (from 1.73 to 46.5% for leaf nitrogen content and 5.56 to 93.8 mm2.mg for SLA) are included in this trait area. Plants belonging to this group similarly range in size from small to huge leaves (0.02 to 590 cm2) and from light to heavy seeds (2.72 to 8272 mg seed mass). Although it was limited to lower SLA values (ranging from 9.09 to 38.2 mm2.mg) and seed mass (ranging from 0.01 to 980 mg), the passive climbing trait space (Figure 2c) also displayed a wide range of trait combinations. However, it did include a wide range of stem-specific density (ranging from 0.3 to 1.3 g cm−3). Out of all the liana species, the only two that displayed a strong phylogenetic signal ($\lambda > 0.8$) were seed mass and stem-specific density.

When comparing species with active climbing to those with passive climbing, functional richness, functional evenness, and functional dispersion were all significantly higher in the

former case. Active and passive climbing species did not considerably enhance the lianas trait space, based on the similar functional contributions. In contrast, it was discovered that passive climbing species had much higher originality (active species originality = 1.46, passive species originality = 1.54).

Environmental variable predictors

Significant variations in the contributions made by various climbing strategies to the patterns of liana biodiversity worldwide were discovered. The majority of plant variety was consistently accounted for by active climbing species on several botanical continents. In comparison to Africa and Southern America, Asia contributed more to plant diversity proportionately to active climbing.

A distinct variance in the richness of the ascending mechanism to gradients of the past (precipitation anomaly) and present (temperature, seasonality, and precipitation). Active climbing had a negative relationship with precipitation anomaly (Est. = -0.13, $p < 0.01$) and a positive relationship with seasonality (Est. = 0.17, $p \leq 0.05$) and precipitation (Est. = 0.20, $p \leq 0.05$). Rather, there was a positive correlation (Est. = 0.10, $p \leq 0.05$) between passive climbing richness and precipitation anomaly, and a negative correlation (Est. = -0.12, $p \leq 0.05$) between the two. Phylogeny drove the abundance of both passive and active climbing species (passive climbing: Est. = -0.28, $p < 0.001$, and active climbing: Est. = -0.20, $p \leq 0.001$). Lastly, phylogeny was found to be the most accurate predictor of both active and passive climbing species, accounting for roughly 44% and 57% of the variance, respectively, in variable significance analysis. According to our variable importance study, the current climate explains 27% of the variance in passive climbing and 31% of the variance in active climbing. For both active and passive climbing, paleoclimate explained 24% and 14% of the total variance, respectively. Surprisingly, vegetation structure only explained 1% of active climbing and 0.2% of passive climbing, making it a poor predictor of climbing mechanism representation.

Study indicates that the type of climbing mechanism is a key characteristic in understanding the functional and taxonomic variety of lianas. Functional diversity measures between climbing species that are active and those that are passive showed a significant difference. The study findings partially confirm the hypothesis that a stronger filter for active climbing is support dependency. Significantly, as evidenced by their decreased richness, dispersion, and originality, the species in this group demonstrated functional convergence towards comparable feature combinations. Furthermore, it was discovered that aggressive and passive climbing systems responded to environmental factors significantly differently. Phylogeny (44%–57%), current climate (27%–30%), paleoclimate (14%–24%), and vegetation structure (<2%) were the main explanations for these reactions. These results substantiate the notion that a bifurcated classification of climbing mechanisms in the lianas can explain considerable variance in their functional and taxonomic richness on a global scale.
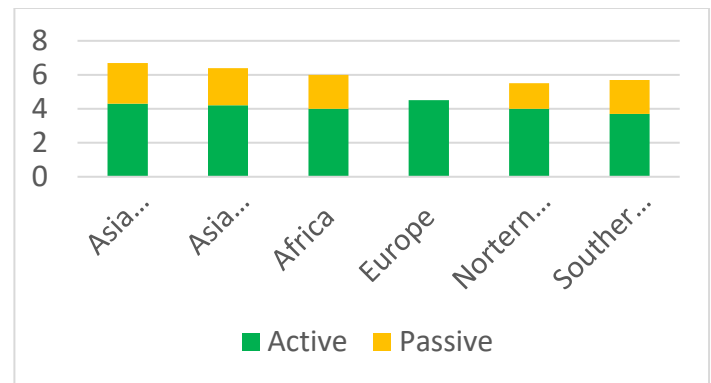

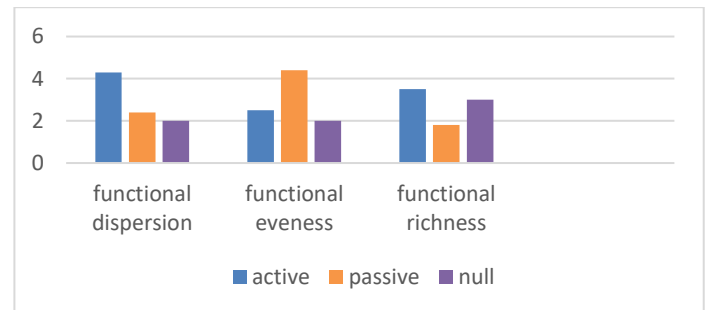Figure 2: Proportional richness of climbing mechanism graph

Figure 3: Climbing mechanisms contribution graph

Functional diversity of lianas differs by climbing mechanisms

Two axes, one representing the plant's size and the other the leaf economics spectrum, can be used to summarize much of the diversity in aboveground features found in plants (Diaz et al., 2016; Laughlin et al., 2020; Sterck et al., 2011; Wright et al., 2004). findings support the significance of these two axes, which together account for 70% of the diversity in the trait space of lianas. On the other hand, passive climbing species are more grouped towards the size spectrum, whereas active climbing species are concentrated towards the leaf economic spectrum. Since active climbers can grow in both exposed high light conditions and shaded understory conditions (Medina-Vega et al., 2021), their higher functional richness suggests that they have explored more niches than passive climbers. In contrast, passive climbers are more likely to be restricted to the shaded understory. In fact, lianas' climbing mechanism determines how far they can grow and how acclimated they can become, both inside and between forests (DeWalt et al., 2000; Putz, 1984; Putz & Holbrook, 1991). Nevertheless, in contrast to trees, the liana's capacity to locate a suitable support is mostly dependent on the rate of stem elongation rather than the investment in diameter increase. For example, studies have shown that lianas (Bai et al., 2020; Ichihashi & Tateno, 2015; Roeder et al., 2012; Schnitzer, 2005) and active species (Teramura et al., 1991) have higher rates of shoot elongation than do trees. The variations in functional traits between the active and passive species it is observed lend credence to the

theory that active climbing species develop more quickly towards completely exposed circumstances in the high forest canopy and get advantages from a more acquisitive approach. Nevertheless, a constraint for macroecological studies of lianas is the limited number of distinct functional variables observed for the same species (Willson et al., 2022). A trait imputation technique was employed to partially overcome this constraint. Consequently, the urgent need for further data on various functional features for the same individuals of liana species is stressed in order to support more reliable evaluations of the a priori climbing mechanism classification that was employed. Complementary characteristics that characterize the extent of several dimensions (or estimations) of diversity include functional richness, evenness and dispersion at the group level, and contribution and originality at the species level (Mouchet et al., 2010). The study findings suggest that in active climbing lianas as opposed to passive ones, support reliance is probably a more potent filter for certain features. For example, compared to the null model, active species displayed decreased originality and lower richness and dispersion, showing functional convergence. This probably reflects the robust external support system that allows active species to flourish. Rather, compared to the null hypothesis, active species displayed increased evenness, suggesting that some characteristic combinations are not more prevalent than others. This implies that in order to investigate the vertical gradient from the low-light forest floor to the high-light canopy, active species are more likely to possess a variety of distinct trait combinations. In fact, compared to passive climbing species, active climbing species have a tendency to reach the canopy and spread over various host crowns, resulting in a more aggressive space occupation strategy (Ichihashi & Tateno, 2015; Isnard & Silk, 2009; Medina-Vega et al., 2021; Rowe & Speck, 2004). An evolutionary and ecological confluence of factors could account for the lower functional convergence of passive climbing lianas. One of the simplest climbing strategies to evolve may be the basic scrambling mechanism, which is widely distributed in the phylogeny of angiosperms and involves few developmental and morphological alterations (Sperotto et al., 2020). As a result of ecological filtering, species possessing a root-climber mechanism seem to be grouped in the wettest regions (Durigon et al., 2013, Speroto et al., 2023). The theory that active climbers fill a broader variety of niches than passive climbers, who are typically confined to the understory of shady forests is supported by these data (Carter et al., 1988; Dias et al., 2019; Ichihashi & Tateno, 2011; Wyka et al., 2013). In conclusion, the study findings show that the ecological range of lianas is determined not only by the type of climbing mechanism but also by the existence of other traits and how those qualities interact with the environment.

Environmental variable predictors and distribution of climbing mechanisms

The relative contributions of active and passive climbing to the worldwide gradient of liana diversity were consistently different, as we discovered. Across all botanical continents, there are generally more active climbing species than passive climbing species. Species that climb passively are, however, comparatively more diverse in tropical Africa and Asia. Surprisingly, forest structure has little bearing on these biogeographical variations in relative richness. For example, this study Index of Vegetation Structure (IVS, canopy height times tree density) was the least significant and lowest predictor of climbing richness, both passive and active climbing. The findings are at odds with a recent study that found a positive correlation between canopy height and the liana species richness from the tribe Bignoniae, which is known for having tendril climbers as its active climbing mechanism throughout the Neotropics (Meyer et al., 2020). The divergent results can be plausibly explained by two factors. Firstly, unlike in the study by (Meyer et al. 2020), a large group of liana species was examined in the study rather than focusing on a single clade. Secondly, it is probable that the distribution of climbing mechanisms was not adequately supported by the vegetation structure, as determined by the IVS. Alternatively, plot-scale data that takes into account the density of trees as well as their individual height and diameter may better reflect the support-dependence of each type of climbing mechanism to the vegetation. Plot-level data research and a continuum from forested to open regions may be used in future studies to evaluate how vegetation structure affects the distribution of climbing mechanisms.

The second hypothesis is supported by the fact that both active and passive climbing mechanisms have a substantial correlation with some of the major climate predictors of species distribution. Temperature seasonality had a negative correlation with passive climbing but a favorable correlation with active climbing. The enhanced ability for acclimatization and phenotypic flexibility of active climbers may be reflected in the positive association between active climbing richness and temperature. In (Carter et al., 1988) conducted an analysis on the photosynthetic acclimatization of lianas. Their findings revealed that passive species were more physiologically acclimated to low-light conditions, whilst active species showed the most physiological flexibility to high-light conditions. When taking into account the climbing strategies of lianas, the findings generally confirm the hypothesis that niches are partitioned among them to climate gradients. In fact, a prior study (Durigon et al., 2013) indicated that the prevalence of root climbers, a passive climbing mechanism, decreases with rising temperatures in tropical locations; however, the conclusions of this investigation also demonstrate that climate filtering accounts for distributional variations between active and passive climbers. Past climate stability, assessed through a precipitation anomaly, significantly impacted both active and passive climbing species. This finding suggests that the Quaternary climate had a significant influence on the distribution patterns of lianas that exist today. Climates that have been comparatively stable over time have been linked to active climbing species (negative correlation with precipitation anomaly). Conversely, species that do not actively climb were positively correlated with anomalies in precipitation. These findings suggest that the current global abundance of climbing species, both active and passive, may be influenced by

significant climate dynamics occurring over extended periods of time. In fact, variations in the distribution of plant growth forms within particular ecosystems are being prompted by changes in global rainfall patterns (Zhang et al., 2019). The study results also suggest that niche lability may differ between passive and active climbing. Evidence of niche conservatism of growth forms (trees, herbs, shrubs, and climbers) throughout forest savanna transitions in Africa exists, despite the fact that examining the effect of niche conservatism (Gorel et al., 2022). The adaptability of climate niches and climbing techniques could offer a fascinating path for comprehending how niche conservatism organizes liana distributions.

The distribution of active and passive climbing methods can be explained by phylogenetic relatedness, which was discovered to be even more significant than climate and paleoclimate. Rather than the convergence of climbing techniques in areas with comparable climates, the higher influence of phylogeny on the representation of active and passive climbing species may be attributed to the small number of lineages that go through local radiations (Sperotto et al., 2020, 2023). For example, when a few families represent species confined in a certain climate or region, this pattern may result from shared ancestry rather than from separate occurrences in the evolution of that climbing mechanism (Sperotto et al., 2023). The study, which made use of the World Checklist of Vascular Plants (WCVP v.2.0, Govaerts et al., 2021), one of the largest botanical databases in the world, showed notable and divergent relationships between the species richness of active and passive climbing mechanisms in the paleoclimate and the current climate. But the number of individuals was not included in the analysis; rather, it only contained data on the occurrence of the species. Taking abundance into account offers a more thorough and nuanced understanding of ecological communities (Keil & Chase, 2019), especially when observing the effects of habitat loss and climate change. Abundance is a crucial component of species diversity. It is proposed that future research could evaluate the generalizability of these findings while simultaneously considering species richness and abundance by utilizing plot-level data on abundance in connection with liana climbing strategies. These investigations will offer the chance to separate the primary factors influencing liana abundance and richness from their reaction to climate change.

IV. CONCLUSION

This research highlights the critical role that climbing mechanisms play in comprehending global trends in the functional diversity and distribution of lianas. Although the evolutionary development of different climbing strategies in lianas has received limited attention, it is vital for understanding their life histories and connecting species' reactions to climate change. In this study, we demonstrated that passive climbing lianas exhibit distinct functional diversity and different patterns in their richness-environment relationships compared to active climbers. In general, filtering related to support dependence and forest vertical structure plays a role in driving functional similarities and differences between active and passive climbing lianas. Furthermore, the Quaternary climate history has left a

more pronounced impact on active lianas, highlighting the significance of past climatic conditions in shaping the present distribution of lianas.

Increasing in the Neotropics, steady in the Afrotropics, and mixed in Indo-Malaysia, the rise in liana abundance and biomass in recent decades has not been consistent throughout the tropics (Schnitzer, 2018; Schnitzer & Bongers, 2011). It is concluded that in order to comprehend such diverse liana responses across continents and their cascading impacts across ecosystems, life history (climbing techniques) and functional features must be taken into account. An enormous opportunity to learn more about the possible mechanisms underlying the species and functional diversity of liana communities and their responses to climate change across tropical forests worldwide has been created by the expansion and accessibility of global data (such as BIEN and TRY in recent years).

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