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Species assemblages and their drivers differ between trees and lianas in a seasonal evergreen forest in Thailand

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Abstract

Despite a long tradition in ecology of studying tree species assembly and its potential drivers in tropical forest communities, little information exists with respect to lianas (woody climbers), the second most abundant life form of woody plants in tropical forests. Lianas influence forest diversity and stability and provide critical resources for forest fauna. Using a unique dataset of a 30-ha plot in Thailand, where tree and liana individuals were fully mapped, we investigated the degree to which local species assemblages of trees and lianas of different size classes (i.e., seedlings, established individuals, and large individuals) are related to local environmental conditions. We asked (1) What are the spatial patterns and environmental drivers of local tree and liana species assemblages? (2) How do such patterns and drivers differ among size classes? (3) Which species associate with these assemblages? Local assemblages of established trees showed substantial structuring by environmental variables, whereas we found only weakly structured assemblages of tree seedlings, large trees, and lianas of all size classes. Our results indicated that the biotic and abiotic drivers of local species assemblages differed strongly between tree and liana communities and across size classes. Species assemblages of trees were

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mainly driven by soil nutrients, leading to patchy assemblages associated with high base saturation (Alfisols) and assemblages associated with lower levels of base saturation and higher aluminum (Ultisols), whereas tree seedling assemblages were only weakly structured by riparian zones. In contrast, species assemblages of established and large lianas were primarily associated with forest canopy structure, separating low-canopy forests from high-canopy forests, whereas soil nutrients were the only factors associated with liana seedling assemblages. The weak environmental structuring of tree seedlings and large trees suggests that other mechanisms, such as stochastic disturbances, competition for space, or animal seed dispersal, may play an important role in structuring tree communities in this seasonal tropical forest. The weak patterns observed in liana communities across all life stages raise questions about the underlying mechanisms of liana community assembly, and further research should focus on liana niches, their dispersal mechanisms, and host tree relations.

KEYWORDS
disturbance, habitat association, indicator species, multivariate regression tree, seedlings, soil nutrients, Southeast Asia, species assemblages, topography

INTRODUCTION

Ecologists have long sought to understand the mechanisms governing tree species assembly in tropical forests by studying the interactions of trees with environmental conditions, neighboring plants, herbivores, and pests, as well as the effects of demographic stochasticity and dispersal limitation (HilleRisLambers et al., 2012). However, there has been much less research on lianas (woody climbers), which comprise up to 30% of the woody species in intact forests (Schnitzer et al., 2015). Lianas are woody climbing plants that compete with their hosts for below- and aboveground resources and use tree stems and branches to grow into the canopy to obtain access to light (Schnitzer et al., 2015; Visser et al., 2018). Lianas may influence forest diversity by stabilizing or destabilizing tree species coexistence by suppressing the competitive dominant or subordinate species, respectively (Schnitzer, 2018). Additionally, lianas provide critical resources such as food, shelter, perching, nesting opportunities, and aerial pathway for forest fauna, particularly arboreal seed dispersers, but they may also suppress certain food resources (Schnitzer, 2018). Although lianas are an important component of tropical forests, we know little about the mechanisms and factors that govern their community assembly and coexistence patterns (Dalling et al., 2012; Liu et al., 2021), and it is not known whether and how local species assemblages of lianas vary in their responses to changing environmental conditions.

The abiotic environment is a major determinant of local community assembly in plant communities (Gunatilleke et al., 2006; Harms et al., 2001; Kraft et al., 2015; Punchi-Manage et al., 2013; Zuleta et al., 2020). Abiotic conditions should be reflected in the spatial distribution of individual species through regeneration niches (Grubb, 1977) and habitat filtering (Kraft et al., 2015; Whittaker, 1956). Furthermore, the spatial distributions of species should combine to form distinct species assemblages of functionally similar species that are associated with specific environmental conditions (Rubio & Swenson, 2022). Studies that quantify the influence of environmental variables on local species assemblages of tropical trees have been conducted with a focus on edaphic drivers such as topography (Allie et al., 2015; Kanagaraj et al., 2011; Punchi-Manage et al., 2013; Zuleta et al., 2020) and soil resources (Allie et al., 2015; Baldeck et al., 2013; Bunyavejchewin et al., 2019; Condit et al., 2013; Russo et al., 2008; Turner et al., 2018; Zekeng et al., 2022). Topography controls the spatial variation in hydrological conditions and affects the spatial distribution of soil moisture and nutrients (Allie et al., 2015), and it is a major driver of forest composition at sites with steep slope gradients (Punchi-Manage et al., 2013). Differences in performance among species in response to soil nutrients may create local assemblages corresponding to edaphic areas with high or low levels of specific nutrients (Turner et al., 2018). Additional variables that can drive local tree species assemblages include forest canopy structure and its variation, which are typically driven by disturbances such as tree-fall gaps and have been proposed as an important mechanism for tree diversity maintenance (Hubbell et al., 1999; Molino & Sabatier, 2001).

Following a climber life strategy, local liana assemblages may primarily depend on the characteristics of tree canopy structure such as gaps (Liu et al., 2021; Schnitzer, 2018). Some species can recruit rapidly and abundantly in gaps due to higher light availability as well as their physiological adaptation to drought (Schnitzer, 2018; Schnitzer et al., 2021). Given that lianas show distinctive functional traits, which differ significantly from those of trees, an interesting question arises—whether liana distribution differs in their association with environmental conditions from that of trees. For example, soil nutrients may also drive liana community assembly, as studies from tropical forests in Panama and China have reported that soil nutrients are good predictors of the distribution of some liana species (Dalling et al., 2012; Liu et al., 2021). However, the relative importance of canopy structure and soil nutrients for liana species assemblage is largely unknown.

The emerging local species assemblages may change with the size of the trees or lianas, as the relative importance of processes such as habitat associations or competition for space may change during their life cycle (Comita et al., 2007; Kanagaraj et al., 2011; Punchi-Manage et al., 2013; Russo et al., 2008). If species differ in their requirements for seedling establishment (i.e., a regeneration niche; Grubb, 1977), the seedlings community should be structured into local species assemblages composed of species with similar environmental requirements. However, we expect that the high year-to-year variability of seed input due to variability in climate (Usinowicz et al., 2017) and variability in abundance and distribution of seed dispersers and predators (Dennis et al., 2005) may mask existing regeneration niches and result in only weak structuring of seedlings into species assemblages. If subsequent survival is mainly associated with environmental conditions, local species assemblages of trees and lianas should become more apparent with increasing size. Conversely, if survival is dominated by negative density-dependent mechanisms or by stochastic disturbances, local species assemblages should become less predictable by environmental conditions with increasing size. The latter is especially likely for larger individuals that face strong competition for space.

Here we examine whether local community assemblages of tropical trees and lianas on the Mo Singto plot, a 30-ha ForestGEO plot in Central Thailand, are environmentally driven and change with size classes. We focus on three size classes, including seedlings because they form the template for all subsequent processes of community assembly and may reflect the regeneration niches (Comita et al., 2007), all established individuals, and large individuals. Large trees are of interest because they are preferably used by large lianas as host. Our specific objectives were to investigate: (1) which aspects of the biotic and abiotic environment (i.e., canopy structure, topography, and soil nutrients) determine local species assemblages of trees and lianas of different size classes; (2) how the strength of emerging species assemblages (environmental determination) differ between size classes and between trees and lianas; and (3) which species are indicators of these assemblages. Our specific hypotheses are summarized in Table 1.

METHODS

Study site and datasets

This study was conducted on the 30-ha (500 × 600 m) Mo Singto ForestGEO plot (Brockelman et al., 2017), located at 101°22′ E, 14°26′ N in Khao Yai National Park, a UNESCO world heritage site in Thailand. The plot is located in intact tropical seasonal evergreen forest at 720–815 m above sea level and has average annual precipitation of 2200 mm and average temperature of 22.4°C (19.4–22.4°C), with a dry season of 4–6 months (Brockelman et al., 2017).

Tree and liana censuses

Based on the ForestGEO standard protocol (Condit, 1998), the plot is divided into 20 × 20 m quadrats and all trees with dbh $\geq$ 1 cm were tagged, mapped, measured, and identified to species, with re-censuses conducted every 5 years. Here we used the tree data of the 2015–2017 census, which matches the period in which environmental variables were collected best. Similarly, we used the liana census that was carried out during 2016–2017. Liana individuals are rooted in the ground, but different branches (ramets) of a liana may climb the stems of different nearby trees. The liana census therefore recorded all ramets with dbh $\geq$2 cm, the location of the host trees of ramets, and the location where the liana was rooted in the ground. We considered ramets growing on different host trees as separate individuals, because they have grown up in different biotic and abiotic environments. The seedlings of trees and lianas were monitored in 2018 during the wet season (July–November), and all tree and liana seedlings with height $\geq$5 cm were tagged and their heights measured.

We considered three different size classes, including seedlings (height ≥ 5 cm and dbh < 1 cm), all established individuals (trees with dbh > 1 cm and lianas with dbh ≥ 2 cm), and large individuals (trees with dbh ≥ 10 cm and lianas with dbh ≥ 5 cm). Because a cutoff size is difficult to justify for trees with multiple stems, we calculated a dbh equivalent by first summing up the basal area of all stems and then converting back into a dbh equivalent. Details on the censuses are provided in Appendix S1.

Environmental variable: Soil nutrients

In total, 250 soil samples were taken during May–June 2017 (see Appendix S2: Figure S1) and analyzed for 26 different forms of nutrients and pH (Table 2; Appendix S2: Table S1) using the standard ForestGEO method (Davies et al., 2021). The results were then extrapolated to the 20 m × 20 m quadrat scale using kriging (John et al., 2007). Our soil variables included eight elements, that is, N, P, K, Al, Mg, Fe, Ca, and Na. Because many of

TABLE 1 Key questions, expectations, and underlying hypotheses.

Questions	Tested variables	Hypotheses and influence of variables	
		Trees	Lianas
Q1: Which aspects of the biotic and abiotic environment determine local species assemblages?	Canopy structure	Moderate: higher proportion of shade-tolerant species in taller canopies[a]	Strong: spatially associated to disturbed areas[b]
	Soil nutrients	Strong: emerging assemblages associated to edaphic conditions[c]	Moderate: emerging assemblages associated to different soil nutrient[d]
	Riparian zones	Weak: only a few riparian species have been reported[e]	Strong: avoiding riparian zones, because grow well under a drier condition (outside the riparian zones)[f]
	Other topographies	Strong: Slope specialists[g]	Weak: no report before
Q2: How does the strength of local species assemblages differ among size classes?	Size classes	Weak → Strong → Weak: Seedlings show low structuring due to high variability in seed input and high mortality, habitat filtering leads to strong structuring of saplings, and negative density-dependent mechanisms (e.g., competition for space) or stochastic disturbances lead to reduced structuring of large trees[g]	Weak → Strong → Strong: Liana seedlings share similar niches with tree seedlings, many lianas can reach to the canopy even if their diameters ~1–2 cm[f]
Q3: Which species are indicators of these assemblages?	Indicator species	Strong: related to soil, canopy structure and topography[g]	Strong: related to canopy structure[f]

[a] Hubbell et al. (1999) and Molino and Sabatier (2001).

[b] Ledo and Schnitzer (2014) and Schnitzer (2018).

[c] Condit et al. (2013) and Turner et al. (2018).

[d] Dalling et al. (2012) and Liu et al. (2021).

[e] Brockelman et al. (2017).

[f] Schnitzer (2018) and Sun et al. (2022).

[g] Kanagaraj et al. (2011), Punchi-Manage et al. (2013), and Sun et al. (2022).

TABLE 2 Habitat groups and variables in each group.

Group	Variable
Topography and its derivatives[a]	Topographic wetness index; curvature; slope; aspect, solar radiation
Soil properties	PCA1 and PCA2 of all soil nutrients (see Appendix S2: Table S1)
Canopy structure[a]	Mean TCH above the 10th, 25th, 50th, 75th, 90th percentile (P10, P25, P50, P75, and P90, respectively), CV of TCH determined at 5 m × 5 m resolution (CV5m), and solar radiation (solar)

Abbreviations: PCA, principal components analysis; TCH, top canopy height.

[a] Variables calculated from LiDAR data at 1 m × 1 m resolution.

the soil variables were highly correlated (Appendix S2: Figure S5), we applied a principal components analysis (PCA) to summarize the information from the 26 soil variables into the first two axes, PC1 and PC2 (Figure 1a; Appendix S2: Figure S3e), which together explained about 66% of the total variation in soil chemistry. Details on the measurement of soil variables are provided in Appendix S1.

Environmental variable: Forest structure

To extract forest structure variables, we used a 1-m resolution canopy height model that represents the top canopy height (TCH), estimated from airborne LiDAR data acquired in April 2017 (Jha et al., 2020). To assess responses to different degrees of disturbances, we calculated five variables for each 20 × 20 m quadrat that capture the variation between mean canopy height and maximum canopy height, including the mean canopy height above the 10th, 25th, 50th, 75th, and 90th percentile. This results in the variables P10 (close to mean canopy height), P25, P50, P75, and P90 (close to maximum canopy), respectively (Figure 1b; Appendix S2: Figure S3f). Low values of P10 and P25 indicate forest gaps, whereas high values of P75 and P90 indicate the presence of tall trees. To additionally capture the variability of the canopy structure, which is related to forest successional stage (Chanthorn et al., 2016), we computed the CV of the TCH at 5-m resolution (CV5m) over each quadrat (Appendix S2: Figure S3d).

Environmental variables: Topography

We used topographic variables similar to those used in previous studies (Kanagaraj et al., 2011;

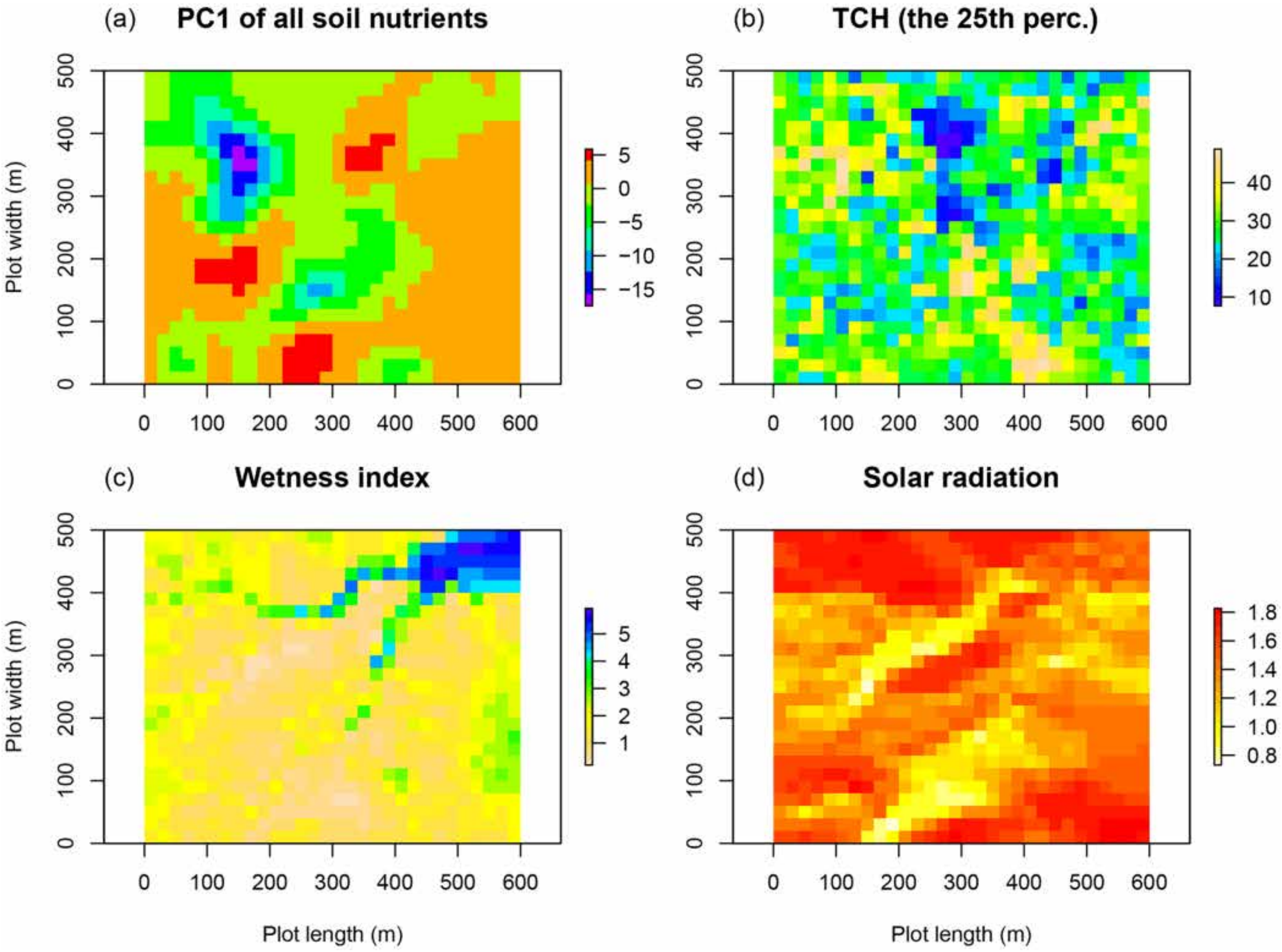

FIGURE 1 Maps (600 m × 500 m) of important variables: (a) principal component (PC) 1 of the soil nutrients; (b) mean top canopy height (TCH) above the 25th percentile (perc.) or P25; (c) topographic wetness index; and (d) solar radiation. The right-side bars of (c) and (d) are in meters and megawatt hours per square meter units, respectively, whereas the others are unitless. Additional variables are shown in Appendix S2: Figure S3.

Punchi-Manage et al., 2013), including slope, sin-transformed aspect, and curvature from a 1-m resolution digital elevation model (DEM) (Jha et al., 2020) (Appendix S2: Figure S3). In addition to these variables, two topography-derived variables, the amount of incoming solar radiation (insolation) (Figure 1d) and the topographic wetness index (Table 2, Figure 1c), were estimated using the SAGA GIS software (http://www.saga-gis.org). The topographic wetness index reflects water flow in a landscape. We used solar radiation because some areas that receive less radiation are densely covered by understory perennial shrubs, which may affect tree seedlings (Chanthorn et al., 2013). Details on the measurement of environmental variables are provided in Appendix S1.

Multivariate regression tree analysis and indicator species

Our objective is to investigate the degree to which distinct local species assemblages emerged in response to local environmental conditions. To this end, the plot is divided into 20 × 20 m quadrats to capture the environmental variation on the 30-ha plot scale (Kanagaraj et al., 2011; Legendre et al., 2009). We then define species assemblages as collections of 20 × 20 m quadrats that show maximal similarity in species composition and maximal dissimilarity to quadrats belonging to other assemblages. To identify such assemblages, we used multivariate regression tree analysis, a hierarchical constrained cluster analysis (De'ath, 2002; Legendre et al., 2009). This analysis determines the environmental variables and their associated thresholds that lead to the maximal contrast (i.e., the largest within-assemblage similarity and the largest among-assemblage dissimilarity).

The analysis proceeds in a stepwise manner (Appendix S2: Figure S2): in the first step, it selects, among all environmental variables, the variable V1 and its associated threshold T1 that lead to the maximal contrast; in the second step, it keeps V1 and T1 and selects, among the environmental variables, the variable V2 and its associated threshold T2 that lead to a new (larger) maximal contrast, and so on. To avoid overfitting, we used a robust pruning algorithm (the 1-SE rule; Baldeck et al., 2013; De'ath, 2002) to stop if additional variables did not sufficiently improve the maximal contrast. Additionally, to avoid difficulties in interpreting results, we constrained the maximum number of assemblages in our main analyses to five.

To quantify the strength of the classification into species assemblages, we used the cross-validated relative error (CVRE) (Borcard et al., 2018), which varies between 0 for perfect segregation of species into disjunctive assemblages, to a value of 1 for a very poor classification. Additionally, we used the coefficient of determination R^2, which is given by one minus the relative error (where the relative error is the sum of the within-assemblage sum of squares over all assemblages divided by the overall sum of squares of the data).

The multivariate regression tree analysis provides thresholds of environmental variables that define the range of environmental conditions of each assemblage. For clearer interpretation, we used this information together with the maps of environmental variables to label each assemblage with a qualitative habitat type. Given that the assemblages are defined by environmental thresholds, we expected to find assemblages related to specific environmental conditions (e.g., a riparian zone is expected to have high values of the topographic wetness index). The remaining quadrats were then related to an unspecific matrix habitat (e.g., nonriparian habitat).

Species that characterize a given assemblage can be identified by an indicator species index, here defined as the product of relative abundance and relative frequency of occurrence of the species within the assemblage (Dufrêne & Legendre, 1997). A species that is perfectly classified (i.e., it appears in all quadrats of the assemblage, but not in any other assemblage) has the maximal indicator value of 1, whereas a species that does not occur in any quadrat of the assemblage gets the minimum value of 0. Following Punchi-Manage et al. (2013), we defined an indicator species if its indicator value was >0.25 and significant with $p < 0.05$, as determined by a test using random permutations of species among quadrats, and using only species with ≥20 individuals per size class. An indicator value >0.25 indicates that the species is present in at least 50% of the quadrats of the assemblage and that its relative abundance in that assemblage reaches at least 50%. Even though they may not be indicator species, they are more associated with the assemblage (based on the indicator value) than randomly distributed species. Details on the regression tree analysis and the indicator species analysis are provided in Appendix S1.

RESULTS

Habitat variation

The distribution of soil nutrients in the study plot was patchy; the first two components of the PCA of our 26 original soil variables showed aggregated and isolated patches of low and high values in different parts on the plot (Figure 1a; Appendix S2: Figure S3e). The canopy structure showed two patches of low-canopy structure in the northern part of the plot (Figure 1b). High values of the wetness index appear along the main streams on the plot, and the large patch on the upper right corner is swampy during the wet season (Figure 1c). Thus, we defined them as "riparian zones." Overall, the habitat of the Mo Singto plot shows locally heterogeneous environmental conditions (Figure 1; Appendix S2: Figure S3).

Species assemblages

Seedlings

Tree and liana seedlings showed very weak structuring into species assemblages: the proportions of explained variation were moderate to low ($R^2 = 0.08$ and 0.02, respectively), and the classification was poor (CVRE = 0.96 and 0.99, respectively) (Table 3a, Figure 2a,d). These results support our hypothesis that seedlings should show weak species assemblages (Table 1, Q2). For tree seedlings, the topographic wetness index separated the riparian zone (TWI > 3; see Figure 1c, Table 3a) from three additional assemblages that were defined by soil nutrients (PCA1) and canopy height (P25), which included an assemblage characterized by low canopy height (i.e., P25 < 15.7). While we expected a weak structuring of the tree seedling community by soil nutrients and canopy structure, the main structuring by the riparian zone was unexpected (Table 1, Q1). In contrast, liana seedlings

TABLE 3 Species assemblages for trees and lianas for (a) seedlings, (b) all established individuals, and (c) large individuals (see also Figure 2).

Variables and assemblages	Tree	Liana
(a) Seedling		
Indiv./spp.	19,925/177	14,411/105
Errors	$R^2 = 0.08$, $R^2_{\mathrm{full}} = 0.1$; CVRE = 0.96, $\mathrm{CVRE}_{\mathrm{full}} = 0.95$	$R^2 = 0.02$, $R^2_{\mathrm{full}} = 0.02$; CVRE = 0.99, $\mathrm{CVRE}_{\mathrm{full}} = 0.99$
Assemblage 1	TWI < 3; PCA1 < 0.6; P25 ≥ 15.7 (Matrix1)	PCA1 ≥ −1 (Matrix)
Assemblage 2	TWI <3; PCA1 ≥ 0.6 (Matrix2)	PCA1 < −1 (Alfisol)
Assemblage 3	TWI < 3; PCA1 < 0.6; P25 < 15.7 (L.canopy)	
Assemblage 4	TWI ≥ 3 (Riparian)	
(b) Established		
Indiv./spp.	131,785/270	9311/131
Errors	$R^2 = 0.39$, $R^2_{\mathrm{full}} = 0.5$; CVRE = 0.66, $\mathrm{CVRE}_{\mathrm{full}} = 0.63$	$R^2 = 0.04$, $R^2_{\mathrm{full}} = 0.06$; CVRE = 0.98, $\mathrm{CVRE}_{\mathrm{full}} = 0.97$
Assemblage 1	PCA1 < 2.1; PCA1 ≥ −1.3 (Matrix)	P25 < 20.7 (L.canopy)
Assemblage 2	PCA1 < 2.1; PCA1 < −1.3 (Alfisol)	P25 ≥ 20.7; PCA1 ≥ −1.9 (Matrix)
Assemblage 3	PCA1 ≥ 2.1; Solar ≥ 1371.2 (Ult.solar)	P25 ≥ 20.7; PCA1 < −1.9 (Alfisol)
Assemblage 4	PCA1 ≥ 2.1; Solar < 1371.2; PCA2 < −2 (Ult.Al-Fe)	
Assemblage 5	PCA1 ≥ 2.1; Solar < 1371.2; PCA2 ≥ −2 (Ult.Al)	
(c) Large size		
Indiv./spp.	15,269/212	3929/118
Errors	$R^2 = 0.09$, $R^2_{\mathrm{full}} = 0.14$; CVRE = 0.94, $\mathrm{CVRE}_{\mathrm{full}} = 0.91$	$R^2 = 0.03$, $R^2_{\mathrm{full}} = 0.03$; CVRE = 0.99, $\mathrm{CVRE}_{\mathrm{full}} = 0.99$
Assemblage 1	PCA1 ≥ −2; Solar < 1452; PCA1 < 1.1 (Matrix)	P10 < 21.3 (L.canopy)
Assemblage 2	PCA1 < −2 (Alfisol)	P10 ≥ 21.3 (Matrix)
Assemblage 3	PCA1 ≥ −2; Solar ≥ 1452 (Ult.solar)	
Assemblage 4	PCA1 ≥ −2; Solar < 1452; PCA1 ≥ 1.1 (Ultisol)	

Note: The table shows the number of individuals and species (Indiv./spp.) in the size class, the R^2 of the regression tree model, and the cross-validated relative error of the multiple regression trees (CVRE and $\mathrm{CVRE}_{\mathrm{full}}$ with and without pruning, respectively). Names in parentheses indicate the habitat types. Alfisol and Ultisol (Ult.) are the habitat types that are mainly associated with base saturation and Al-Fe, respectively. Ultisol has three subgroups separated by high (Ult. solar) and low solar radiation consisting of Al and Fe (Ult.Al and Al-Fe [Ult.Al-Fe]). L.canopy is a habitat type characterized by low canopy height (P10 and P25). The matrix habitat type is what remained and was not directly related to variables.

Abbreviations: PCA, principal components analysis; TWI, topographic wetness index.

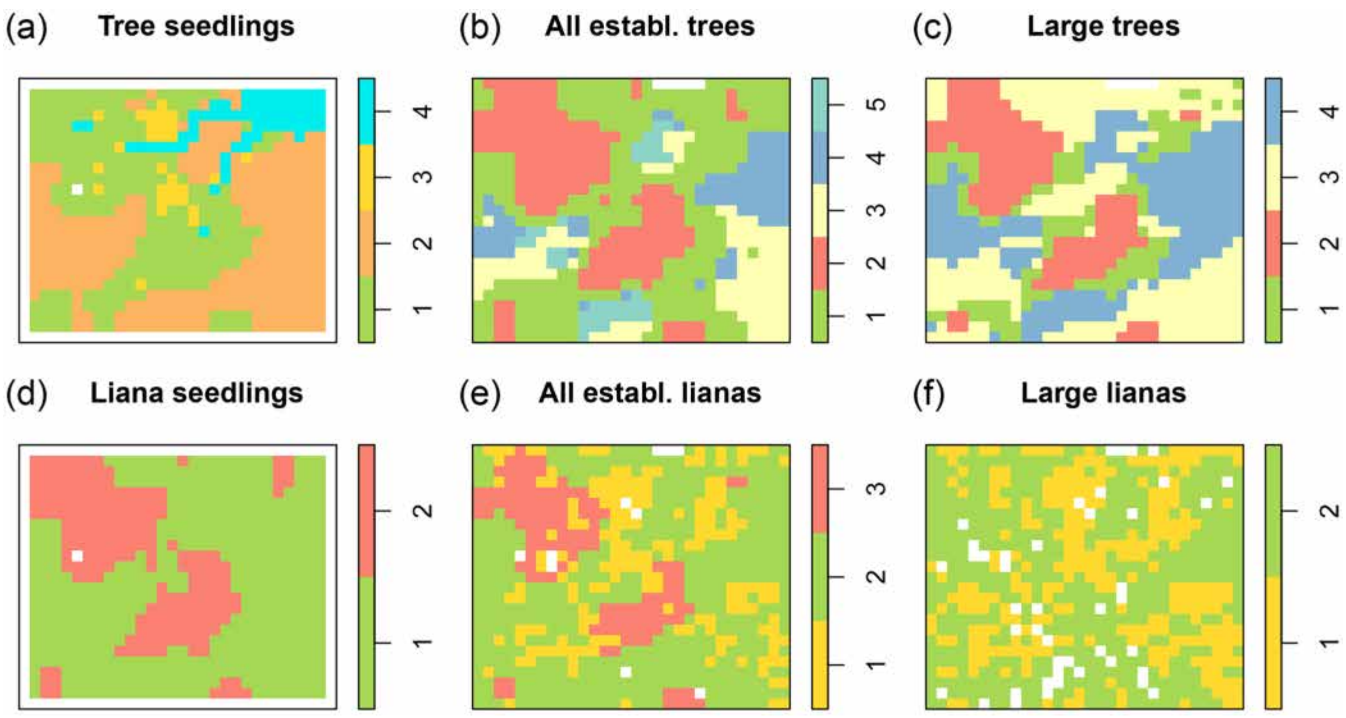

FIGURE 2 Map of community assemblages of seedlings, all established (establ.) individuals (all establ. trees and lianas), and large individuals of trees (a–c) and lianas (d–f) in the Mo Singto plot (600 m × 500 m). The side bars indicate the corresponding assemblages on the map (the variables of the regression trees and their splits are shown in Table 3), where the same panel color represents assemblages with a similar threshold. The resolution of one pixel (quadrat) is 20 m × 20 m. White pixels are quadrats without any individual, including the removed quadrats of secondary forest.

showed only two weak species assemblages driven by soil nutrients (PCA1).

Established individuals

Established trees showed five species assemblages (Figure 2b, Table 3b) with substantially lower classification error than the seedling assemblages (i.e., CVRE = 0.66), thus supporting our hypothesis that all established trees (which are mostly small trees) should show stronger species assemblages (Table 1, Q2). The species assemblages of established trees were mainly driven by soil nutrients (PCA1) and to a lesser extent by solar radiation (solar): Assemblage 2 was associated with low values of PCA1 (i.e., $\text{PCA1} < -2.1$), Assemblages 3, 4, and 5 were characterized by high values of PCA1 (i.e., $\text{PCA1} \geq 2.1$), whereas Assemblage 3 was subdivided by high incoming solar radiance (i.e., >1371 kWh/m^2). The community of small trees (1–10 cm dbh) showed similar species assemblages as the community of all established trees (Appendix S2: Table S2). These results support our hypothesis on the main role of soil nutrients in structuring the community of small trees, but could not support the hypothesized impact of canopy structure (Table 1, Q1).

Established lianas showed three assemblages (Figure 2e), but the classification was weak (Table 3b). As expected (Table 1, Q1), the species assemblages of established lianas were mainly driven by a variable of canopy structure (P25) and soil nutrients (PCA1). Assemblage 1 was characterized by low values of canopy height (i.e., $\text{P25} < 20.7$), which indicates gap or disturbed habitats, whereas the remaining two assemblages were characterized by low values of soil PCA1 (i.e., $\text{PCA1} < -1.9$; Assemblage 3) and by high values of soil PCA1 (i.e., $\text{PCA1} \geq -1.9$; Assemblage 2).

Large individuals

Large trees were structured into four assemblages (Figure 2c, Table 3c), but as expected (Table 1, Q2), they showed a higher classification error (CVRE = 0.94) than established trees (Table 3b,c). This result was not driven by the smaller sample size of large trees as confirmed by a rarefaction analysis (Appendix S1 and Appendix S2: Figure S4). As with all established trees, the main structuring variables for large trees were the first PCA of the soil variables and solar radiation. Assemblage 2 of large trees (brown area of Figure 2c) was similar to Assemblage 2 of established trees (Figure 2b), Assemblage 2 of liana seedlings (Figure 2d), and Assemblage 3 of established liana (Figure 2e). Large lianas showed two assemblages with high classification error (Table 3c) driven by canopy height (Figure 2f), with Assemblage 1 being characterized by gaps or disturbed habitats.

Interpretation of soil-related species assemblages

Soil variables structured all tree and liana size classes to some extent (Table 3). We therefore use the results of the PCA for a rough assessment of the soil type of the soil-driven species assemblages. Figure 3 shows the two-dimensional space spanned by the two first components of the PCA of the 26 soil variables, the loading of the different soil nutrient variables, and the main areas of the PCA1 variable that characterize the different assemblages (i.e., the green, white, and yellow area). Quadrats with large values of PCA1 (located in the yellow area) show high values of saturated aluminum and low values of base saturation (BS) and are characterized by Ultisol. Assemblages 3, 4, and 5 of established trees and Assemblage 4 of large trees belong to this soil type. Quadrats with large negative values of PCA1 (i.e., PCA1 < -1.3, -2) show high values of BS and low values of saturated aluminum and are characterized by Alfisol. Assemblage 2 of large trees, established trees, and liana seedlings, and Assemblage 3 of established liana belong to this soil type; they are shown in brown color in Figure 2.

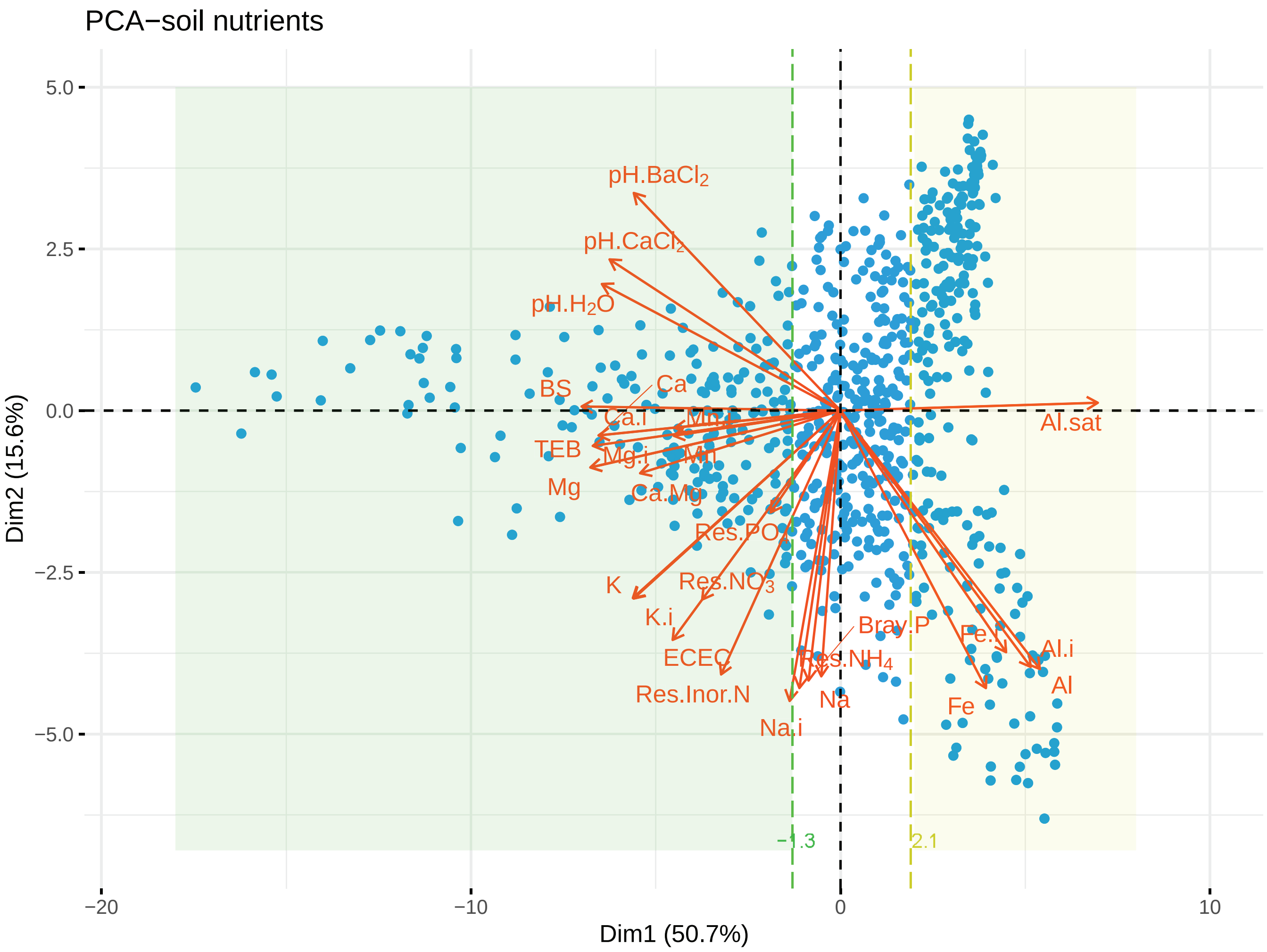

FIGURE 3 Principal components analysis (PCA) of the 26 soil variables and interpretation of soil-related species assemblages. Location of the 750 quadrats in the biplot defined by the first two principal components of the soil variables (blue circles) and the corresponding loadings of the soil nutrient variables (arrows). The green shaded area corresponds to quadrats with high base saturation (PCA1 < -1.3), characterized by Alfisol, whereas the yellow shaded area corresponds to quadrats with high Al and Fe but low base saturation (PCA1 > 2.1), characterized by Ultisol. The unshaded area is a matrix transition area. The details of soil nutrients are described in Appendix S2: Table S1.

Indicator species

Overall, only between 2% and 11% of all species in a given size class of trees and lianas were indicator species (Figure 4; Appendix S2: Table S3). These percentages are not very different from what we would expect by chance with a rejection probability of 0.05 (~5%). Established trees had the highest proportion of indicator species (11%), followed by liana seedlings (5%). With exception of established trees, the number of indicator species of a given assemblage was low (≤5), and some assemblages did not show any indicator species (Figure 4; Appendix S2: Table S3). Nevertheless, the soil-related assemblages (2, 3, and 5) of established trees showed high numbers of indicator species (7, 14, and 8, respectively, Appendix S2: Table S3), and Assemblage 3 of liana seedlings (i.e., PCA1 < 1) showed five indicator species (Appendix S2: Table S4). Given these low numbers, and our relatively low weak criterion for definition of an indicator species (i.e., the species must only be present in 50% of the quadrats of the assemblage), there is little evidence for our hypothesis of environmentally driven indicator species in this tropical forest (Table 1; Q3).

Although only a few species qualified as indicator species, we found that at least 16%–38% of all species had a significant association with an assemblage (i.e., "significantly associated" species; Figure 4; Appendix S2: Tables S3 and S4). Except established trees, all other size classes of trees and lianas showed a low number of significantly associated species (Figure 4).

DISCUSSION

Local species assemblages are expected to emerge in response to local variability in environmental conditions

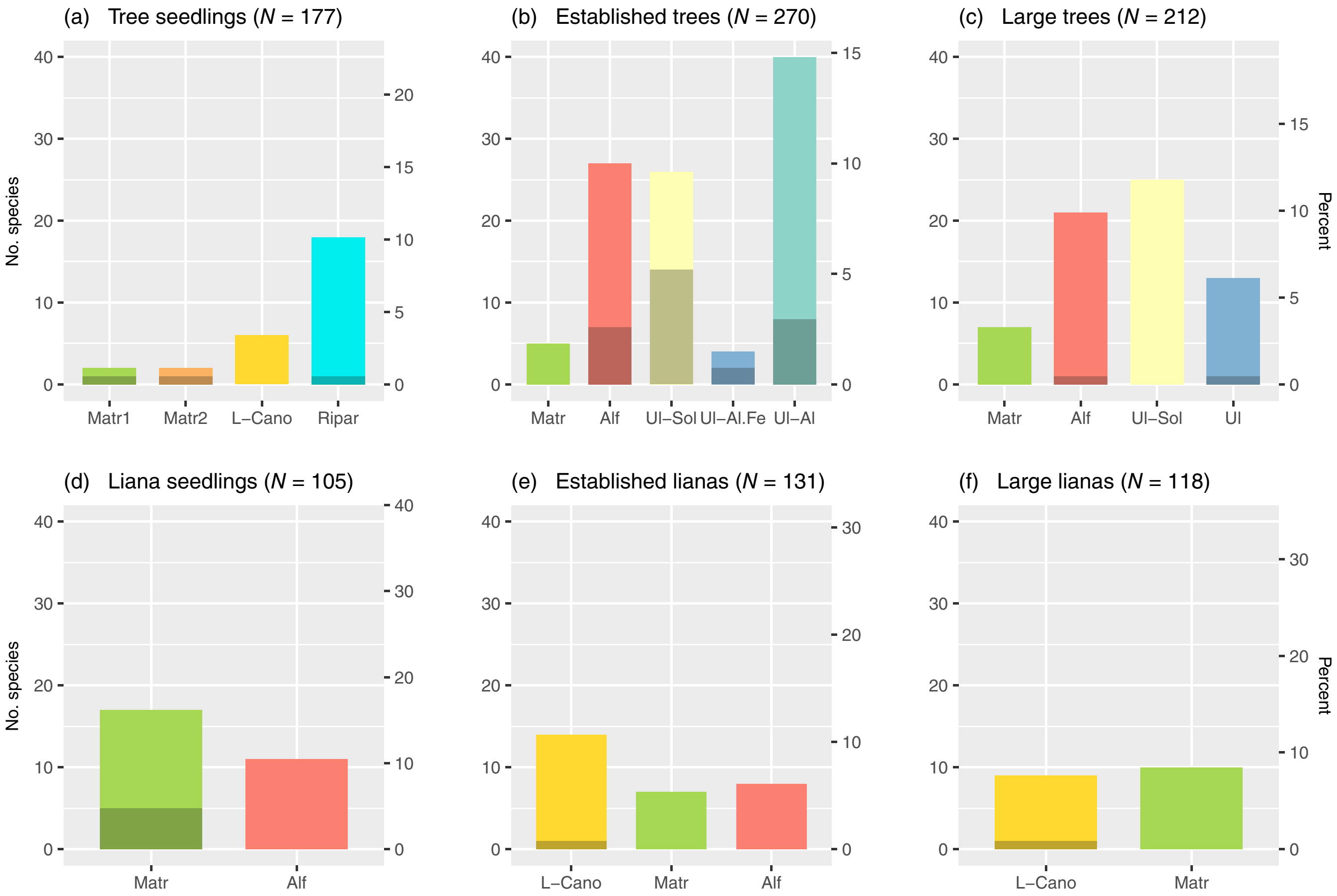

FIGURE 4 Number of species (the left vertical axis) and percentage of total species (the right vertical axis) of significantly associated (nonshaded bar) and indicator species (shaded bar) for the different size classes and species assemblages. Indicator species have more than 20 individuals, an indicator value >0.25, and a randomization test significant at $p < 0.05$. Significantly associated species show $p < 0.05$. N is the total number of species. Alfisol (Alf) and Ultisol (Ul) are the habitat types that are mainly associated with base saturation and Al-Fe respectively. Ul-sol is the habitat type with high solar radiation, whereas Ul-Al and Ul-Al.Fe are low solar radiation type consisting of Al and Al, Fe. L-Cano is a habitat type characterized by low canopy height (P10 and P25). Ripar is a riparian habitat type indicated by the topographic wetness index. The matrix habitat types (Matr) are what remained and were not directly related to variables.

(Kanagaraj et al., 2011; Rubio & Swenson, 2022). Here we used multivariate regression tree analysis to investigate the degree to which local species assemblages of trees and lianas of different size classes in a tropical forest in Thailand were related to local environmental conditions. In contrast to our expectations, we found that lianas of all size classes were only weakly structured into environmentally driven species assemblages, whereas most results of trees confirmed our expectations on changes in the strength of structuring into species assemblages with tree size. While tree seedlings showed low structuring, habitat filtering leads to substantial structuring of small trees, which is then lost in large trees. Nevertheless, we found several environmental variables that significantly structured the local species assemblages in interpretable ways. Finally, our indicator species analysis showed that species were not strictly confined to individual habitats, but that environmental conditions rather modulated their densities among habitats.

Community assembly

We observed the emergence of environmentally driven species assemblages, and the predictive error of the regression tree was relatively high (Table 3). This result agrees with studies in tropical forests at Barro Colorado Island (BCI) in Panama (Kanagaraj et al., 2011) and the Sinharaja tropical forest in Sri Lanka (Punchi-Manage et al., 2013). However, we need to place these figures into context. An R^2 of the regression tree close to one (or a CVRE close to zero) would mean an almost perfect segregation of species into disjunctive assemblages. As habitat associations usually provide only a (slight) performance advantage in their preferred habitat (Allie et al., 2015; Bartlett et al., 2016; Johnson et al., 2017), it will lead most likely to different densities of species among habitats, but only rarely to species that are strongly confined to individual habitats. Additionally, seed dispersal, especially by animals (Brockelman et al., 2017), may lead in the Mo Singto plot to a substantial "spillover" of species among assemblages, which dilutes the relationship between species and environment in sufficiently connected habitats (Réjou-Méchain & Hardy, 2011; Shmida & Wilson, 1985). Thus, even a relatively low R^2 value, such as that of all established trees, indicates structuring of the tree community into environmentally driven species assemblages.

Role of soil nutrients

Our results show that soil nutrients were the most important environmental variables that drive local species assemblages of trees in the Mo Singto plot (Table 3). Similar results were reported from studies in many tropical rain forests of Southeast Asia (e.g., Bunyavejchewin et al., 2019; Paoli et al., 2006; Russo et al., 2008), and we could additionally identify local species assemblages characterized by different soil taxonomy (Brockelman et al., 2017). While phosphorus is expected to drive species assemblages in tropical forests (Condit et al., 2013; Turner et al., 2018), our study underlines the key role of BS (Figures 2, 3 and Table 3). The assemblage characterized by high BS was associated with Alfisol (i.e., large negative values of PCA1; Figure 3), whereas assemblages characterized as Ultisol showed low levels of BS (i.e., large values of PCA1; Figure 3), due to greater leaching, and high values of Al and Fe that tend to make the soil more acidic (Appendix S2: Figure S5) (Brockelman et al., 2017; Fujii et al., 2018).

The two main patches of high BS were located in two basins near the longest downhill ridge on the west, where two small streams join (one of them is a seasonal stream), and may be created by leaching from the ridge into the basins (Allie et al., 2015). These two patches were associated with assemblages of large and established trees (Assemblage 2 in Figure 2b,c). We also found an Alfisol assemblage of liana seedlings and all established lianas, which, however, disappeared for large lianas (Figure 2d–f). The presence of this soil pattern in liana seedlings suggests that lianas occupying these areas share similar nutrient resources with established and large trees (Figure 2b,c). Given that the Alfisol assemblage appears already at the earlier stage of lianas, it is rather unlikely that it arises through association with host tree species.

As aluminum is toxic to the plant metabolism, species associated with Ultisol should have benefited from evolutionary adaptations that enable them to mitigate the toxicity of aluminum (Zemunik et al., 2018), or they may have short root length due to low concentration of aluminum in the surface soil (Rehmus et al., 2017). Assemblages 3–5 of established trees and Assemblage 4 of large trees were driven by this soil type (Figure 2b,c). Furthermore, the proportion of indicator species associated with Ultisol assemblages was highest for established trees (Figure 4b), supporting the hypothesis of plant adaptation to the toxicity of aluminum.

Changes in environmental determination with size class

Our analysis confirmed our expectation of changes in the environmental determination of tree species assemblages with size class (changing from weak to strong and back to weak again; Figure 2, Table 3). We found only a low environmentally driven structuring in tree seedlings ($R^2 = 0.08$, Table 3), mainly driven by topographic wetness, which divided the seedling community into riparian versus nonriparian assemblages, and by soil nutrient and canopy structure. Seedlings were therefore not subject to stronger habitat filtering and did not show pronounced regeneration niches, but their effects could also be overpowered by stochasticity in seed input (Usinowicz et al., 2017) or by spatiotemporal variability in seed dispersers (Dennis et al., 2005). However, in accordance with studies at BCI (Kanagaraj et al., 2011) and Sinharaja (Punchi-Manage et al., 2013), the class of all established trees (dominated by that of small trees; Appendix S2: Table S2) showed the most pronounced structuring into species assemblages (Table 3b).

The weakening of emerging species assemblages in large trees suggests that additional processes, such as competition for space or a greater exposure to severe disturbances, counteract the advantage of being in habitats optimal for earlier stages as tree size increases. Notably, the higher explained variability for small trees compared with large trees was not driven by the lower density of large trees, as shown by our rarefaction analysis (Appendix S2: Figure S4).

We found an Alfisol assemblage (high BS soil) instead of an expected canopy-related assemblage in the liana seedling stage, but not in large lianas (Figure 2, Table 3). This suggests that liana seedlings may survive in the low-light conditions under host trees during the free-standing or early climbing phases. This adaptation may also be an explanation for the long-term increase in liana seedlings seen in the Panama site, which was explained neither by canopy nor moisture conditions (Umana et al., 2020). However, the Alfisol assemblage disappeared for small (Appendix S2: Table S2) and larger lianas (Table 3), suggesting that their eco-physiological mechanisms respond to the open and dry conditions in a forest gap (Schnitzer, 2018).

The role of canopy structure

Canopy gaps are prominent features of tropical forests and key to their dynamics (Hubbell et al., 1999; Molino & Sabatier, 2001). An assemblage characterized by areas of low canopy height appeared for tree seedlings (Figure 2a), but no variables representing gap-related structures structured the assemblages of all established trees and of large trees (Figure 2b,c). This departure from our expectation is probably due to most gaps not being large enough, or closing too early, to enable the recruitment of pioneer species in the larger size classes. For example, *Choerospondias axillaris*, a long-lived pioneer species on our plot, can recruit in forest gaps, but seedlings cannot survive to the mature stage (Chanthorn & Brockelman, 2008). Alternatively, as all established and large trees recruited earlier in such gaps, the canopy rapidly closed.

Compared with trees, lianas have the life history advantage of being able to perform better in disturbed habitat, such as forest gaps, and in drier conditions (Chen et al., 2015, 2017; Schnitzer, 2018). As expected, forest disturbance was the most important driver of liana community assembly, as also shown in a recent study from BCI (Schnitzer et al., 2021). A declining trend of precipitation on the Mo Singto plot during the last 25 years (Brockelman et al., 2017; and unpublished meteorological data) may presage drier conditions on the plot, which may make lianas more competitive in the forest canopy (Medina-Vega et al., 2021). Notably, this prediction assumes little difference in liana strategy along a gradient of canopy openness.

The variable that represents average canopy height above the 25th percentile (>20 m) was selected as the main variable driving liana species assemblages (Figure 2, Table 3). Low-canopy forest (<20 m), maintained by competition from sprawling lianas, may remain stable for three to four decades (Brockelman, personal observation). This may explain the arrested succession on large plots as seen in Panama (Schnitzer & Carson, 2001) and French Guiana (Tymen et al., 2016). If these arrested-succession patches are stable or expanding, they may ultimately suppress gap-phase regeneration, as reported for Barro Colorado (Schnitzer et al., 2021).

In contrast, a high proportion of species associated with typical canopy height of intact habitat (i.e., mean of canopy height >20 m; Figure 4e,f) suggests that tree size is also an important variable for liana species assemblages (Mori et al., 2016; Yang et al., 2018). Thus, lianas of these assemblages are not suppressed by large trees, for example, through competition for space. This is in line with a study on liana succession in the same area that reported an increase in both liana numbers and sizes relative to tree sizes (Lomwong et al., 2023). Thus, different liana species may have different ecological niches with respect to forest structure: the niche of one group being a more disturbance-structured habitat, and the niche of the other consisting of smaller gaps in more intact forest. These findings suggest that not all lianas follow a life history predicted by the “seasonal growth advantage” hypothesis where they perform best in open and drier habitats (Schnitzer, 2018). Additionally, only a single indicator species, *Uncaria scandens*, associated with low-canopy assemblage was found. We have often observed this species in persistent forest gaps. Thus, some lianas may be low-canopy specialists, while others may be generalists or weak-to-moderate Alfisol specialists (otherwise the Alfisol assemblage would not have emerged).

Role of topographic variables and riparian habitat

Topography is generally assumed to be the major determinant of species distributions and community patterns at scales of tens of hectares (e.g., Bunyavejchewin et al., 2019; Kanagaraj et al., 2011; Punchi-Manage et al., 2013; Valencia et al., 2004; Zuleta et al., 2020). In contrast, our results suggest an indirect role of topography via solar radiation and soil moisture (wetness) variation. Although light has long been known as a major limiting resource in tropical forests, only a few studies have reported on the effects of topography on incoming radiation (Hubbell et al., 1999; King et al., 2005; Stark et al., 2015). We initially expected that incoming solar radiation and canopy disturbance would be the major drivers of seedling assemblages, particularly for lianas (Schnitzer, 2018). Only a single pioneer tree species (*Eugenia syzygioides*, out of 14 associated species) was significantly associated with this assemblage (Appendix S2: Table S3).

In contrast to liana seedlings, tree seedlings were most affected by the topographic wetness index (TWI), and 10.2% of the tree seedling species was associated with riparian habitat (Figure 3). This implies that a large proportion of tree seedling species may be highly sensitive to drought. A study at Barro Colorado (Panama) showed that many tree species had increased mortality in extreme drought years (Browne et al., 2021). These results raise an important concern for the coming era of more frequent and severe droughts (Cai et al., 2014).

CONCLUSIONS

Although lianas are taxonomically similar to trees, they differ from trees in important life history strategies and influence the diversity and stability of forests (Schnitzer, 2018). This study compared the degree to which tree and liana communities are structured into environmentally driven species assemblages. We found large differences between the tree and liana communities. While trees showed species assemblages similar to those found in other tropical and subtropical forests (e.g., Guo et al., 2017; Kanagaraj et al., 2011; Punchi-Manage et al., 2013; Rodrigues et al., 2020; Wang et al., 2017), liana assemblages of all size classes showed only weak structuring. This points to fundamental differences in structure and functioning between tree and liana communities. Nevertheless, although liana assemblages were generally weak, it is interesting to note that liana seedlings and all established lianas share the Alfisol assemblage with established and large trees. Overall, our results suggest that lianas are not as strongly dependent on their biotic and abiotic neighborhoods as are trees, most likely because of their climber life strategy that requires flexibility in the selection of structural support needed to gain access to light. The relatively weak patterns found across size classes raise questions about the strength of community assembly in lianas. A study comparing leaf functional traits between trees and lianas on the Mo Singto plot revealed relatively low variation across all traits in lianas compared with trees (Pothasin et al., 2022), potentially indicating lower niche partitioning and the formation of fewer assemblages. Liana niches, their dispersal mechanisms, and host tree relations are topics that need further research.

AUTHOR CONTRIBUTIONS

Wirong Chanthorn and Thorsten Wiegand conceived and designed the study. Warren Y. Brockelman, Zhenhua Sun, and Anuttara Nathalang designed and conducted the censuses. Wirong Chanthorn analyzed the data with input from Thorsten Wiegand, Rajapandian Kanagaraj, and Maxime Réjou-Méchain. Wirong Chanthorn and Thorsten Wiegand wrote the first draft of the manuscript. All authors read the manuscript and critically provided feedback.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Chanthorn et al., 2024) are available from Zenodo: https://doi.org/10.5281/zenodo.11593871.

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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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