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ORIGINAL ARTICLE

Lianas shift towards larger sizes and more acquisitive trait values in an Asian tropical rainforest

Qi Liu[1,2] | **Frank J. Sterck**[1] | **Jiao-Lin Zhang**[2] | **Lourens Poorter**[1]

[1]Forest Ecology and Forest Management Group, Wageningen University and Research, Wageningen, The Netherlands

[2]CAS Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Mengla, China

Correspondence
Qi Liu, Forest Ecology and Forest Management Group, Wageningen University and Research, P.O. Box 47, Wageningen 6700 AA, The Netherlands.
Email: chn-liuq@outlook.com

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Abstract

Global change is impacting forests worldwide, leading to shifts in forest dynamics and functional composition. We evaluated the changes in the liana community and trait composition over a five-year period (2014–2019) in a Chinese tropical rainforest and assessed the underlying putative mechanisms. We monitored >20,000 lianas in a 20-ha plot, and analyzed community changes for each of the 20 1-ha plots. To identify the putative drivers underlying community change, we used community-weighted mean (CWM) trait values of 18 functional traits that are important for liana performance. During the 5-year period, liana density decreased by 12.6% because of the high mortality of small lianas, whereas liana basal area increased by 5.8% because of the high growth of large lianas. After 5 years, liana communities showed a shift in trait values indicating that they changed towards more large, acquisitive lianas with rapid water use. The temporal shift from slow to fast community trait spectra in carbon, nutrient, and water use was also supported by shifts in the individual CWM traits, from conservative tough leaves towards more acquisitive and water-spending leaves with higher K concentration, leaf thickness, and vessel diameter. Overall, we found no support for a role of disturbances or drought as drivers of the observed changes in the studied liana community. Instead, our study implies that CO_2 fertilization should be considered to better understand dynamics in liana communities in tropical forests.

Abstract in Chinese is available with online material.

KEYWORDS
climbers, demography ecosystem functioning, functional composition, functional traits, global change, liana community, plant–climate interactions, tropical forest

1 | INTRODUCTION

Global change is impacting ecosystems worldwide, threatening biodiversity and ecosystem services (Bradshaw et al., 2009). Understanding how ecosystems respond to global change is critical to improve predictions and making informed management decisions about conservation and climate change mitigation. We focus on tropical rainforests because they store 25% of the terrestrial carbon (Bonan, 2008) and harbor over 50% of the global biodiversity (Myers et al., 2000).

Lianas (i.e., woody vines) play a crucial role in these tropical forests because they comprise a quarter of the woody species (Schnitzer et al., 2012) and contribute up to 40% to forest leaf area (Wright et al., 2004). Lianas reduce the growth and abundance of trees (Peña-Claros et al., 2008) and, hence, forest ecosystem productivity and carbon storage (van der Heijden et al., 2015). Surprisingly, most studies that monitor tropical forest dynamics have focused on trees whereas the role of lianas tends to be overlooked, probably because lianas are only monitored in a few plots

(Schnitzer, 2018). Recent studies found an increase in liana density in multiple Neotropical forests, which has been attributed to a combination of global and local factors (e.g., Laurance et al., 2014; Phillips et al., 2002). Several factors may explain the increase in lianas, such as stronger seasonal droughts, increasing disturbance, and higher atmospheric CO_2 concentration and nutrient deposition (Phillips et al., 2002; Schnitzer, 2018). In Africa, liana abundance also increased in Ghana, probably due to a decline in rainfall (Addo-Fordjour et al., 2021), but it decreased in Democratic Republic of Congo, probably because a local driver (i.e., reduced disturbance by forest elephants) overruled the effects of global change drivers (Bongers et al., 2020). The lack of consensus on liana changes and their underlying drivers urges for additional studies covering a wider geographic range (Gerolamo et al., 2018). Here we present data on liana change in a forest in Xishuangbanna, SW China, because it belongs to one of the five major tropical rainforest regions in the world (Corlett & Primack, 2006), it is part of a global biodiversity hotspot (Myers et al., 2000) and because very few liana dynamics studies have been carried out in Southeast Asia (but see Wright et al., 2015). We evaluate whether changes in the liana community are accompanied by changes in their functional traits. Such a functional trait approach may allow us to infer whether changes in liana abundance and dominance are caused by changes in local drivers (i.e., disturbance) and global drivers (e.g., droughts, CO_2 and nitrogen fertilization) (Esquivel-Muelbert et al., 2019; van der Sande et al., 2016).

The responses of plants to global and local change are largely shaped by their functional traits, because they influence plant recruitment, growth, and survival (Violle et al., 2007). There is a global spectrum of plant strategies, ranging from 'slow' species with conservative trait values (e.g., a low specific leaf area, SLA) that increase resource conservation and plant survival, to 'fast' species with acquisitive trait values (e.g., high SLA) that increase light capture and growth (Díaz et al., 2016; Poorter & Bongers, 2006). The average trait values of a plant community are considered indicators of how plants respond to global change (Soudzilovskaia et al., 2013) and drive community dynamics (Poorter et al., 2017). To our knowledge, our study is the first that simultaneously evaluates changes in liana abundance, basal area, and trait composition.

Here, we evaluated liana dynamics in a 20-ha tropical rainforest over a 5-year period in Xishuangbanna, SW China. We determined the population change of the liana community at individual and basal area levels. We addressed the following questions: (1) How is the liana community changing in terms of stem density and basal area? We expected that after 5 years the liana community would have increased in density and basal area, because increasing CO_2 concentration and nitrogen deposition would lead to increased resource availability, recruitment, and growth. (2) Are these changes accompanied by changes in the functional traits of the liana community? We hypothesize that increased resource availability (e.g., CO_2, nitrogen, or light) would shift the community-weighted mean towards more acquisitive trait values that can make use of these resources, whereas increased drought or shade would lead to communities with traits related to conservative water use.

2 | METHODS

2.1 | Study area

The study was carried out in the 20-ha Xishuangbanna Forest Dynamics Plot in Yunnan Province, Southwest China (21°37′ N, 101°35′ E). The area is characterized by a mean annual temperature of 21.8°C and rainfall of 1475 mm (1980–2019). More than 80% of the precipitation occurs during the rainy season from May to October. The dry season is dominated by cloudy conditions (Cao et al., 2006). The annual amount of fog drip is 89.4 mm, contributing ca. 5% to the annual rainfall, with 86% of this fog drip occurring in the dry season, which is an important additional input of water to this seasonal rain forest during the dry season (Liu et al., 2004). The vegetation is a tropical seasonal rainforest with a canopy height of up to 60 m (Zhu, 2006). A 20-ha permanent plot was established in 2007 based on a standardized protocol (Condit, 1998). The plot measures 400 × 500 m and covers an elevation gradient from 709 to 869 m above sea level, with three perennial streams joining in the plot. The plot is embedded in a national nature reserve. Before 1965, a small area was cleared for agriculture (<0.2 ha, <1% plot area) in one plot corner and thereafter abandoned. Since 1965, no large-scale anthropogenic or natural disturbances have been registered, with the exception of a small landslide (0.04 ha) in 2013 (Liu, Sterck, Medina-Vega, et al., 2021). During the monitoring period (2014–2019) there were very few small scales (<0.1 ha) natural tree falls, and there were no significant directional changes over time in local CO_2 concentrations and rainfall (Appendix S1).

2.2 | Data collection

From August 2013 to March 2014, all rooted lianas with stem diameter ≥1 cm were tagged, mapped, identified, and measured for their stem diameter following a standard census method (Gerwing et al., 2006; Schnitzer et al., 2008). We spatially mapped the rooting point of each liana, which is defined as the last substantial rooting point before the stem ascends. We labeled and mapped the largest "principal stem" and additional multiple stems as described by Gerwing et al. (2006) and measured the diameter at 130 cm from the rooting point at the soil surface. Only when lianas branched below 130 cm (but ≥40 cm from the roots), we measured the diameter 20 cm below the branching point. There were lianas with multiple stems in our study, but their roles seem to be functionally equivalent in the dynamics and effects on trees, and therefore they are treated as separate individuals in the analysis (Schnitzer & Carson, 2001). All multiple stems with a diameter ≥1 cm and that ascended the canopy were recorded. We included all liana species with woody or fibrous perennial stems (e.g., *Desmoncus*, *Gnetum*, *Smilax*, *Dioscorea*), but excluded epiphytes, hemi–epiphytes, and climbing bamboos (Gerwing et al., 2006; Schnitzer et al., 2008). A second census was done circa 5 years later (December 2018–March 2019). Dead individuals were recorded, living individuals were measured for stem diameter at the same marked position, and newly recruited individuals (diameter ≥1 cm) were recorded. To quantify the changes in the liana community between 2014 and 2019 in density and basal area, we subdivided the 20-ha plot into 20,100 × 100 m plots. Population changes were determined for all lianas ≥1 cm diameter in these 20 1-ha plots.

To quantify liana community trait compositions, we selected 29 of the common liana species that had at least 3 individuals to measure functional trait values. These liana species represent ca. 64% of the whole liana individuals and ca. 65% of the liana basal area in the plot, both for all lianas (≥1 cm stem diameter) and for large lianas (≥7 cm stem diameter). Although we did not quantify the trait value of the whole community, we feel it provides a fair description of the community trait values, as the remainder of the species is rare and therefore unlikely to affect the community weighted mean. For each species, on average 8 individuals (range 3–12) with a diameter ≥1 cm were randomly selected from the plot database (231 individual samples in total) to avoid selection bias. Branch and leaf samples were collected between October 2018 and December 2018. From each individual, a ca. 40 cm long branch was sampled from the main stem. As it is difficult to access the lianas in the forest canopy, we followed the standard trait collection procedures (following Pérez-Harguindeguy et al., 2013) by collecting sun-exposed branches. We collected branches between 3 and 8 m in height, as often liana branches drop from the top. Only healthy-looking, sun-exposed, and pest-free leaves were sampled. In case the branch did not have enough leaves for all analyses, additional branches were collected from the same individual to obtain additional leaves. We measured 18 functional leaf-, stem-, and root traits that are considered important for liana performance and liana responses to potential drivers of liana change (i.e., disturbance, drought, and CO_2 fertilization, Table 1). Included traits were leaf thickness (LT), leaf area (LA), specific leaf area (SLA), leaf dry matter content (LDMC), leaf density (LD), vein density (VD), stomatal density (SD), stomatal length (SL), stomatal pore index (SPI), leaf nutrient (nitrogen, phosphorus, potassium, magnesium, and zinc) concentration, leaf N:P ratio (N:P), wood density (WD), vessel diameter (VesDiam) and specific root length (SRL). All trait measurements were made following protocols outlined by Pérez-Harguindeguy et al. (2013). For more details about the collection and measurements of these morphological and anatomy traits, see Liu et al. (2021b). An overview of all sampled liana species with sample size, mean values, and coefficient of variation can be found in Table S1.

2.3 | Data analysis

All statistical analyses were performed using RStudio and R 3.6.2 (R Core Team, 2019). To compare the liana community between the two census periods, a paired *t*-test was done, using the 20 1-ha plots as replicates. For each 1-ha plot, all liana individuals were assigned to 10 mm wide diameter size classes, but individuals with a diameter ≥100 mm were pooled in one class. Paired *t*-tests were done for each class to test for community changes.

Population change and vital rate were determined at the community level for all lianas with diameter ≥1 cm for each of the 20 1-ha plots. To examine the temporal changes in population density, we calculated density change (DC): the ratio of the abundance in 2019 over the abundance in 2014, then ln-transformed DC into lnDC according to suggestions from Bongers et al. (2020). Annual mortality rate (MR) was calculated as $1-\left(N_{ST}/N_0\right)^{1/T}$ (Sheil et al., 1995), where N_0 and N_{ST} refer to the number of individuals recorded in the initial census and the number of surviving individuals present in the final census, respectively. T is the interval period in years. Annual recruitment rate (RR) was calculated as $1-\left(N_{ST}/N_T\right)^{1/T}$ (Sheil 1998), where N_T is the number of individuals recorded in the final census. Average liana diameter growth values were calculated by averaging diameter growth across all individuals. For those individuals, average diameter growth rate (mm yr^{-1}) was calculated as $\left(DBH_2-DBH_1\right)/T$, where DBH_2 and DBH_1 are the diameter of the individuals at the final and initial census, respectively. Similar variables were calculated using total basal area rather than the number of individuals. Basal area-based annual mortality rate was calculated as $\left(BA_D/BA_0\right)/T$, where BA_0 refers to the basal area of individuals recorded in the initial census, the BA_D refers to the basal area of death individuals that were present in the final census and T is the interval period in years. Basal area-based annual recruitment rate was calculated as $\left(BA_R/BA_0\right)/T$, where BA_R is the basal area of new individuals present at the final census period. Average basal area growth rate (mm^2 yr^{-1}) was calculated as $\left(BA_2-BA_1\right)/T$, where BA_2 and BA_1 are the basal area of the individuals at the final and initial census, respectively. Generalized linear mixed model analysis was used to test which demographic process contributes to the community changes by using demographic rates as fixed factors, subplots (1-ha plot) as a random factor, and mortality, recruitment, and growth as predictor variables.

We additionally calculated the demographic parameters for each diameter class. To do so, the proportion of liana density and basal area gain and lost for each liana diameter class were calculated. First, based on the liana census data (density and basal area) in the year 2014, *mortality* was calculated as the dead individuals proportions, *constant*$_{2014}$ means the proportion of survival individual (after 5 years) growth cannot reach to next classes, *outgrowth* accounts the proportion of survival individual (after 5 years) growth reach to bigger classes; second, based on the census data in the year 2019, *recruit* accounts the proportion of recruit individuals, *constant*$_{2019}$ means the proportion of individual growth (in the past 5 years) cannot reach to next classes, *ingrowth* accounts the proportion of recruit individual growth from lower classes (in the past 5 years).

For the functional trait analysis, we compiled a data set with species mean values for all measured plant traits. We then calculated for each of the 20 1-ha plots the community-weighted mean (CWM) trait values for 2014 and 2019, based on the average trait values of the 29 selected species. Species-specific trait values were weighted by the relative density and basal area of each species in the corresponding year (i.e., 2014 and 2019). CWM traits were calculated for each trait in each plot as $CWM_k=\sum_{i=1}^{S}a_{ik}t_i$, where a_{ik} is

TABLE 1 Overview of 18 functional traits.

Trait name	Units	Abbreviation	Measurement and calculation (per individual)
Leaf thickness	mm	LT	3 leaves, central part of the leaf without major veins
Leaf area	mm^2	LA	3 leaves, fresh leaves without the petiole (excluding rachis for compound leaves) ln-transformed for a normal distribution
Specific leaf area	$mm^2 mg^{-1}$	SLA	3 leaves, dividing leaf area by leaf dry mass based on whole leaf excluding petiole and rachis
Leaf dry–matter content	$mg g^{-1}$	LDMC	3 leaves, dividing leaf dry mass by leaf fresh mass based on whole leaf excluding petiole and rachis
Leaf density	$mg mm^{-3}$	LD	1/(SLA × LT)
Vein density	$mm mm^{-2}$	VD	4 images from 1 to 3 leaves, total length of minor veins per unit area
Stomatal density	# mm^{-2}	SD	4 images from impression method from 1 leaf, total number of stomata per unit area
Stomatal length	Mm	SL	4 images, 5 stomates per image, average length of stomata
Stomatal pore index ($SL^2 \times SD$)		SPI	$SD \times SL^2$
Leaf nitrogen concentration	$mg g^{-1}$	N	Standard requirement for technical measurement, nutrient concentration per unit weight
Leaf phosphorus concentration	$mg g^{-1}$	P	Standard requirement for technical measurement, nutrient concentration per unit weight
Leaf potassium concentration	$mg g^{-1}$	K	Standard requirement for technical measurement, nutrient concentration per unit weight
Leaf magnesium concentration	$mg g^{-1}$	Mg	Standard requirement for technical measurement, nutrient concentration per unit weight
Leaf zinc concentration	$mg g^{-1}$	Zn	Standard requirement for technical measurement, nutrient concentration per unit weight
Leaf nitrogen to phosphorus ratio		N:P	Dividing leaf N by leaf P
Wood density	$g cm^{-3}$	WD	1 branch segment, dividing stem dry mass by stem fresh volume
Vessel diameter	µm	VesDiam	1 branch segment, 4 images, 10 largest vessels per image, average diameter of vessels
Specific root length	$m g^{-1}$	SRL	2–3 samples (third branch order of fine roots) root length per unit root dry mass

Note: Units, abbreviations, measurement and calculation were given.

the relative density or basal area of species *i* in plot *k*, t_i is the traits value of species *i*, and *S* is the number of selected species.

Prior to testing whether CWM traits change over time, we tested for spatial autocorrelation among the 20 1-ha plots by using Moran's I (MI) tests. MI value is the slope of the line that best fits the relationship between neighboring variable values and each polygon's target values in the dataset. Hence, the values will be between −1 (perfect dispersion) and 1 (perfect cluster). For each trait we calculated ΔCWM trait change $(CWM_{2019} - CWM_{2014})$ and its relative change (%, $(CWM_{2019} - CWM_{2014}) / CWM_{2014} \times 100$) between 2014 and 2019. For absolute changes in CWM, four out of 18 density-weighted traits showed significant spatial autocorrelation (MI value for SRL = 0.17; LA = 0.18; SPI = 0.18; Mg = 0.33; Table S3), and one out of 18 basal area-weighted traits (MI for LA = 0.16; Table S3). For relative changes in CWM, only two density-weighted traits (MI for SPI = 0.19; Mg = 0.32; Table = S2) showed significant spatial autocorrelation. Hence, only 7 out of 72 comparisons were significant and MI was low (<0.33 in all cases), indicating that there is little spatial autocorrelation in the data, and we therefore treated all 1-ha plots as independent data points.

Please note that we measured species functional trait values only once, in 2018. Changes in CWM trait values between 2014 and 2019 are therefore only driven by changes in species relative abundance/basal area and not by changes in species-specific trait values due to acclimation.

To evaluate how CWM traits are associated and vary over time, a principal component analysis (PCA) was carried out using the 18 CWM traits in 2014 and 2019 as variables and using the 20 1-ha plots as data points. To compare multivariate trait changes between both census periods, a paired samples *t*-test was carried out using both PCA components (PC1, PC2). To evaluate how CWM traits change over a 5-year period, we tested relative changes for each individual CWM trait to see whether its shift significantly differed from zero by using a *t*-test.

3 | RESULTS

Average liana density declined 12.6% over 5 years, from 1158 to 1012 individuals ha^{-1} (paired *t*-test, $df = 19$, $t = -3.77$, $p < .001$) and liana basal area increased by 5.8% from 22.8 m^2 to 24.1 m^2 (paired *t*-test, $df = 19$, $t = -4.50$, $p < .001$, Figure 1). At the community level, changes in density and basal area increased with recruitment and decreased with mortality (Table 2).

In small diameter size classes, liana density decreased significantly from 2014 to 2019, with a net loss of 18% in the 10–20 mm diameter class, 22% in the 20–30 mm diameter class, and 12% in the 30–40 mm diameter class. In large diameter size classes (≥70 mm), lianas increased by 41% over 5 years (Figure 2a). Similarly, liana basal area decreased by 12% in the small-size classes (diameter < 40 mm) and increased (by 46%) in the large-size classes (Figure 2b). The contribution of mortality to density decline decreased from 37% for the 10–20 mm size class to 16% for the 90–100 mm size class, while the contribution of outgrowth to density decline increased from 22% to 68% (Figure 3a). Recruitment contributed to liana increase in the first four size classes, varied from 49% to 0.05% with diameter increase while the contribution of ingrowth to liana increased from 36% in the smallest size class to 89% in the largest size class (Figure 3b). Qualitatively similar patterns were found for the contributions of these vital rates to basal area decline (Figure 3c) or increase (Figure 3d).

The liana functional composition was analyzed for 20 1-ha plots using a principal component analysis (PCA) of 18 density-weighted CWM traits. The first PCA axis (PC1) explained 45.7% of the trait variation across liana communities and showed a slow–fast spectrum in carbon, nutrient, and water use (Figure 4a). Communities at the left were characterized by 'slow' trait values as they had relatively tough and persistent stem tissues (e.g., WD) and leaf tissues (e.g., LDMC) that conserve carbon and nutrients. Communities at the right side were characterized by 'fast' trait values, since wide vessels (VesDiam), large stomata (SL) and a high specific leaf area (SLA) facilitate water, light, and nutrient use, and high leaf nutrient concentrations enable high metabolic activity and growth. The second PCA axis (PC2) explained 25.8% of the trait variation across liana communities and showed a spectrum in water use and uptake and in protein synthesis and activation (Figure 4a). Communities at the top were characterized by 'fast' water use as they had relatively large stomata (SL). Communities at the bottom were characterized by increased water and nutrient capture, protein synthesis and activation as they had high specific root length and high leaf Zn and Mg concentrations. Over the 5-year period, liana communities increased in the axis scores on PC1 and PC2, which indicates that communities became more acquisitive in terms of carbon, nutrient, and water use (Figure 4c; Figure S1). At the same time, liana communities downregulated the capacity to capture water and soil nutrients with lower SRL and leaf Zn and Mg concentrations. Interestingly, communities that were acquisitive in carbon, nutrient, and water use at the start of the monitoring period (i.e., communities at the right quadrant) showed the largest changes over time, whereas conservative communities with low scores (left quadrant) showed little change over time (Figure 4c). The temporal shift from slow to fast community trait spectra in carbon, nutrient, and water use was also supported by shifts in the individual CWM traits. Acquisitive CWM traits that increase carbon, nutrient, and especially water use (e.g., VesDiam, K, SL, and LT) increased significantly over time whereas conservative traits (e.g., SD, LD, LDMC and venation density) and SRL and Zn decreased over time (Figure 5a; *t*-test, $p < .05$ in all cases). A PCA based on basal area-weighted CWM trait values showed similar trait spectra, with PC1 explaining 39.3% of the community trait variation and PC2 explaining 20.2% (Figure 4b). Over the 5-year period, communities also showed an increase in PC1 and PC2 axis scores of the basal area weighted trait values (Figure 4d, Figure S1), and similar changes in CWM trait values (Figure 5b).

4 | DISCUSSION

Tropical forest dynamics may be affected by local disturbances, increased drought stress driven by climate change and/or fertilization

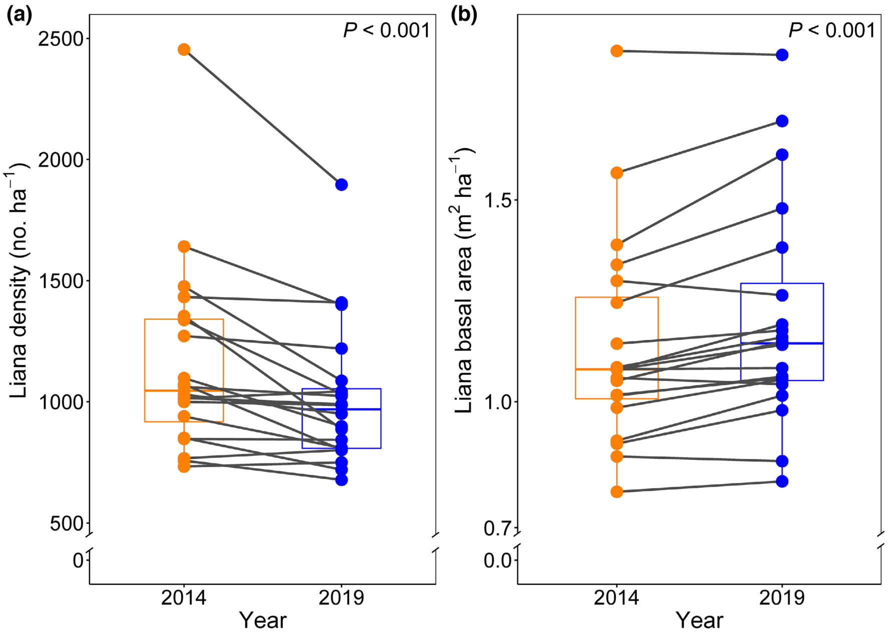

FIGURE 1 Changes in liana community structure in a seasonal tropical rain forest in Xishuangbanna, SW China. Density (a) and basal area (b) per hectare are shown for two censuses (2014 and 2019). Each dot represents absolute density or basal area in a 1-ha plot ($N = 20$). Gray lines connect the measurements of the same plot. Significance levels (*p*) of a paired samples *t*-test are shown.

TABLE 2 Effect of recruitment, growth, and mortality on changes in liana density and basal area.

	Fixed factor				Random factor		
	Name	Parameter Estimate	SE	z-Value		Variance	SD
Density change	(Intercept)	0.008	0.006	1.42	(Intercept)	7.9×10^{-7}	0.0008
	Recruitment	0.052	0.001	90***	Subplot	2.3×10^{-6}	0.0015
	Growth	0.002	0.006	0.27			
	Mortality	−0.053	0.0001	−272***			
Basal area change	(Intercept)	0.190	0.044	4.355***	(Intercept)	5.47×10^{-5}	0.0074
	Recruitment	0.093	0.026	3.54***	Subplot	1.86×10^{-4}	0.0136
	Growth	0.027	0.053	0.52			
	Mortality	−0.047	0.004	−12.14***			

Note: Parameter estimates of the fixed effects are from GLMM models. Subplot (1-ha) is treated as a random factor. *z*-value: estimate/SE; ****p* < .001.

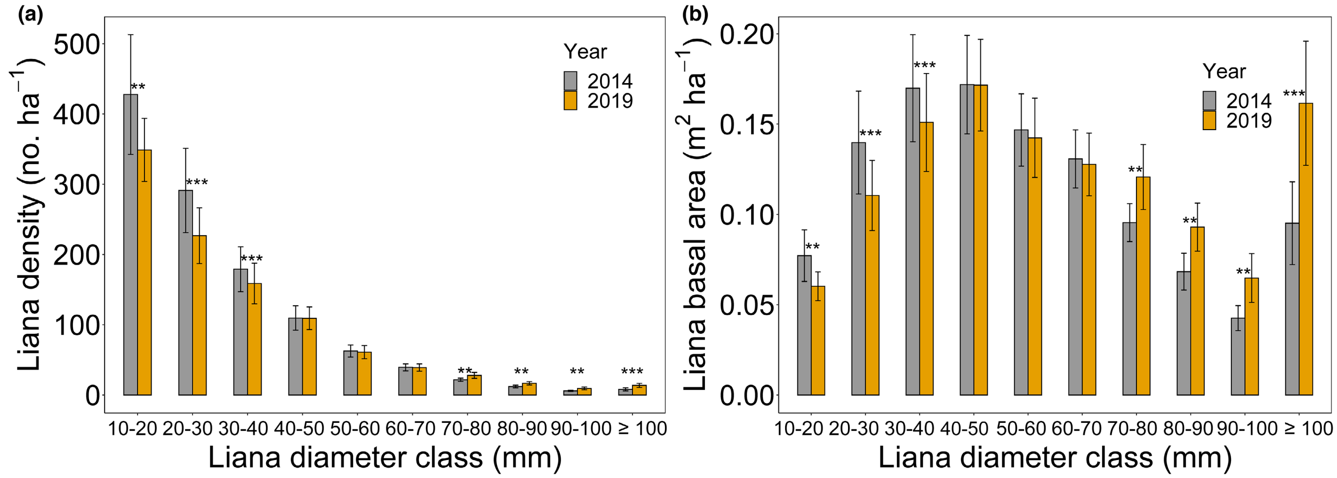

FIGURE 2 Mean (± *95% confidence interval*) of liana density (a) and basal area (b) per diameter class in 20 1-ha plots in Xishuangbanna tropical seasonal rain forest, SW China. In grey, data from the first census (2014, *N* = 23,155); in orange, data for the second census (2019, *N* = 20,231). Asterisks indicate for a given diameter class whether there are significant differences between censuses, based on a paired samples *t*-test (*N* = 20 1-ha plots). ** indicates *p* < .01, *** indicates *p* < .001.

through increased CO_2 and nitrogen deposition. For a liana community in a Southeast Asian forest, we found that overall liana density decreased and basal area increased between 2014 and 2019. Both density and basal area decreased in small-sized lianas but increased in larger-sized lianas.

The decline in liana density was mostly driven by the mortality rate. Mortality rate is the vital rate with the strongest impact on liana density, because it can affect lianas in all size classes and therefore the whole liana population. In contrast, recruitment can only affect the youngest size classes and has therefore less effect on the liana population, whereas increases in liana basal area were also caused by ingrowth (Table 2, Figure 3). The increase towards more large lianas was accompanied by a shift towards more acquisitive traits that reflect rapid water use.

Changes in the liana community were accompanied by shifts in functional properties (Figure 4). An earlier study on the same liana community revealed how liana recruitment and mortality were driven by differences in functional properties (Liu et al., 2023). Specifically, fast carbon and nutrient use increased mortality, while fast water use led to a higher recruitment rate and lower mortality rate. The temporal shift from slow to fast community trait spectra in carbon, nutrient, and water use may, therefore, cause the higher turnover rates occurring in the smallest size classes. This is because the acquisitive species increasing especially for newly established individuals and in small size classes and such species are known to be often less well-defended, more susceptible to pests, pathogens, and natural hazards (Kitajima and Poorter, 2010). Meanwhile, the accumulation of basal area in the large individuals may be caused by the effective water and nutrient acquisition of such species as well, and the high growth rates were apparently not compensated by high mortality in those large-size classes.

The temporal shift of functional properties is here discussed in light of possible drivers, including disturbance, droughts, CO2 fertilization, and nitrogen deposition.

4.1 | Disturbance

At first sight, these liana dynamics suggest that the liana community is undergoing succession after a major disturbance, where growth leads to an increase in basal area but mainly in larger individuals (Figures 1

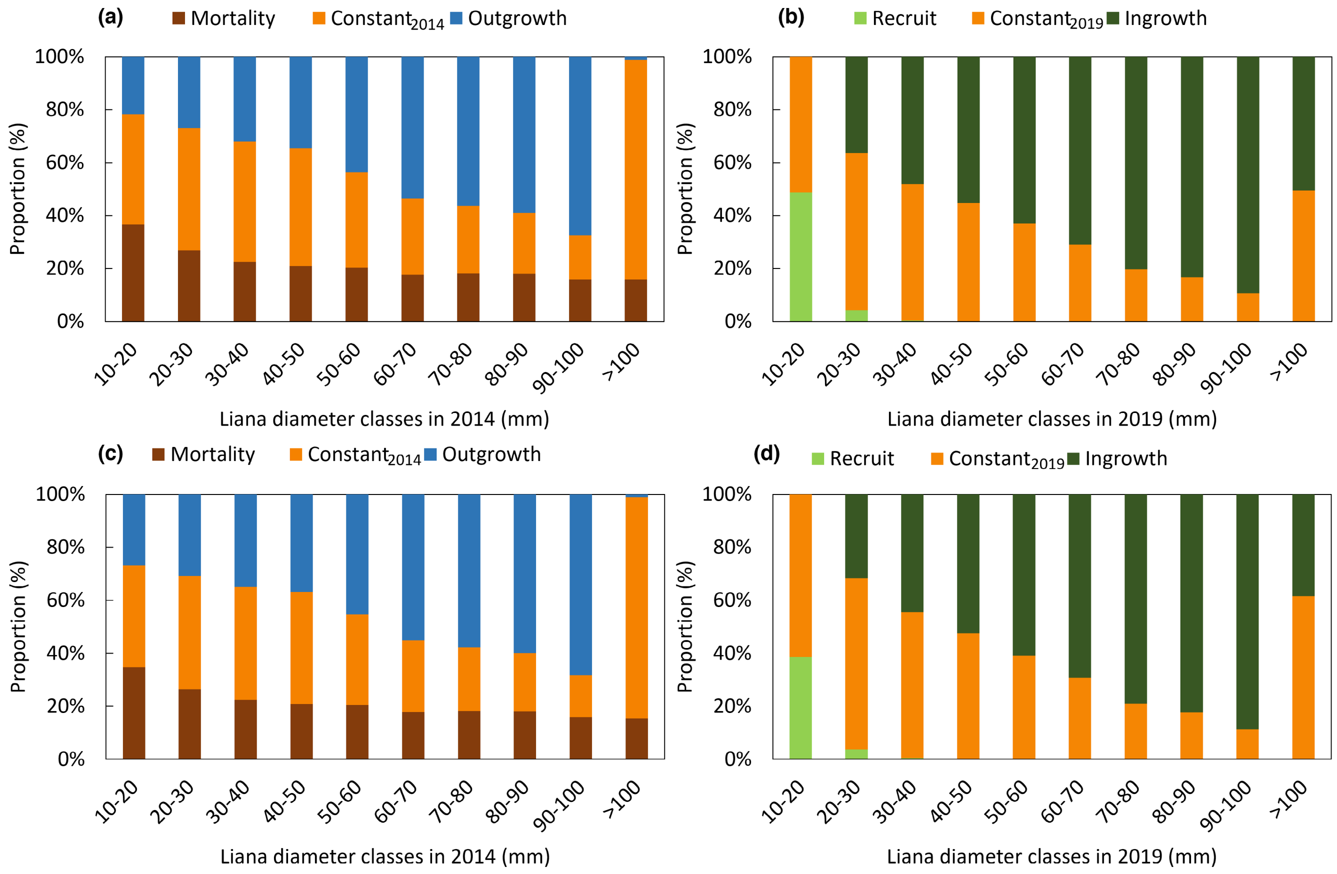

FIGURE 3 The proportion of liana density and basal area gain and lost for each liana diameter class in 20 1-ha plots in Xishuangbanna tropical seasonal rain forest, SW China. In panels (a, c), the proportions were calculated based on the liana diameter class composition in the year 2014, Mortality (brown) means the dead individual proportions, constant2014 (orange) means the proportion of individual growth cannot reach to next classes, outgrowth (blue) accounts the proportion of individual growth reach to bigger classes; in panel (b, d) the proportions were calculated based on the liana density and basal area in year 2019, recruit (light green) accounts the proportion of recruit individuals, *constant*$_{2019}$ (orange) means the proportion of individual growth cannot reach to next classes, ingrowth (dark green) accounts the proportion of recruit individual growth from lower classes. There are 2 individuals in class (>100 mm) showed outgrowth because of mistakes in diameter measurements.

and 2), which likely in turn results in shading and self-thinning of smaller individuals and a decrease in overall liana density (Figures 1 and 2). This is also confirmed by the fact that especially in the smaller size classes mortality contributes to declines in liana density and basal area, whereas, in the larger size classes ingrowth contributes to liana increase (Figure 3). Such changes following major disturbances in the past have been observed for liana communities in Congo and India (Ewango, 2010; Pandian & Parthasarathy, 2016). Yet, to our knowledge, our mature forest did not experience any large-scale disturbances during the 49 years prior to the first census. During the study period only a few tree-fall gaps were formed, which do create a favorable environment for the establishment of pioneer lianas (Schnitzer & Carson, 2001), but these lianas only contribute to recruitment in the smallest size classes and have little effect on overall liana community change, especially in terms of basal area (Figure 3). From this, we argue that the liana community changes in our forest can only to a limited extent be explained by local disturbances over the past 5 decades.

4.2 | Droughts

An increase in the frequency and severity of drought is often mentioned as a reason for liana increase. The reason is that lianas are thought to have a dry-season growth advantage over trees because they invest less in a self-supporting stem but more in deeper roots (but see Smith-Martin et al., 2020) and have access to more water during drought (Chen et al., 2015). Drought is not likely to have played a role in our study forest because (1) it has not experienced strong drought stress during the past decades (Figure S2a), (2) there is not a reduction in rainfall over time (Figure S2a), (3) fog occurrence in the dry season may mitigate dry-season drought stress (Liu et al., 2004), and (4) liana communities changed towards trait values reflecting more rapid water use (Figures 4 and 5; Figure S1). These results imply that drought cannot explain the observed dynamics in the liana community.

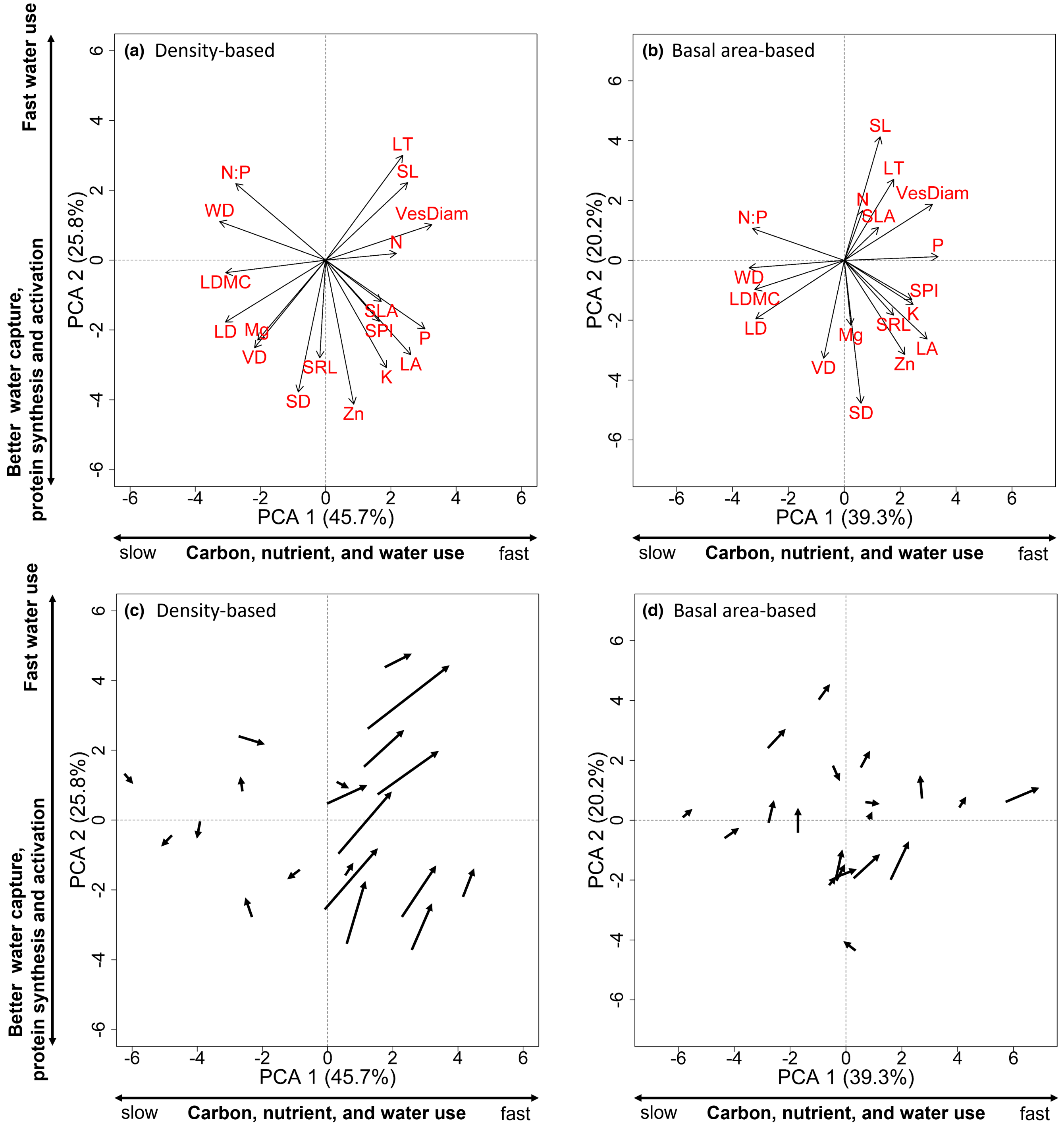

FIGURE 4 Principal component analysis (PCA) of community weighted mean (CWM) traits of 20 liana communities in 2014 and 2019 in a tropical seasonal rain forest in Xishuangbanna, SW China. The first two PCA axes are shown, reflecting variation in slow to fast carbon, nutrient, and water use (PC1). The top panels and labels represent CWM trait loadings weighted by relative density (a) and relative basal area (b). In panels (c and d), the arrows show for each plot the change of PCA axes loading scores over the 5-year period with the arrow pointing towards the last census. Eighteen traits were analyzed: leaf thickness (LT), leaf area (LA), specific leaf area (SLA), leaf dry matter content (LDMC), leaf density (LD), vein density (VD), stomatal density (SD), stomatal length (SL), stomatal pore index (SPI), leaf nutrient (N, P, K, Mg, and Zn) concentration and leaf N:P ratio (N:P), wood density (WD), vessel diameter (VesDiam), and specific root length (SRL).

4.3 | CO_2 and nitrogen fertilization

Fertilization in CO_2 and nitrogen may cause communities to become more acquisitive over time. For nitrogen, such shifts may include a greater leaf area, specific leaf area and a lower leaf dry matter content (Shovon et al., 2020). While the global atmospheric CO_2 concentration has increased steadily over the past decades (e.g., NOAA Climate. gov), the CO_2 concentration at our site did not change much

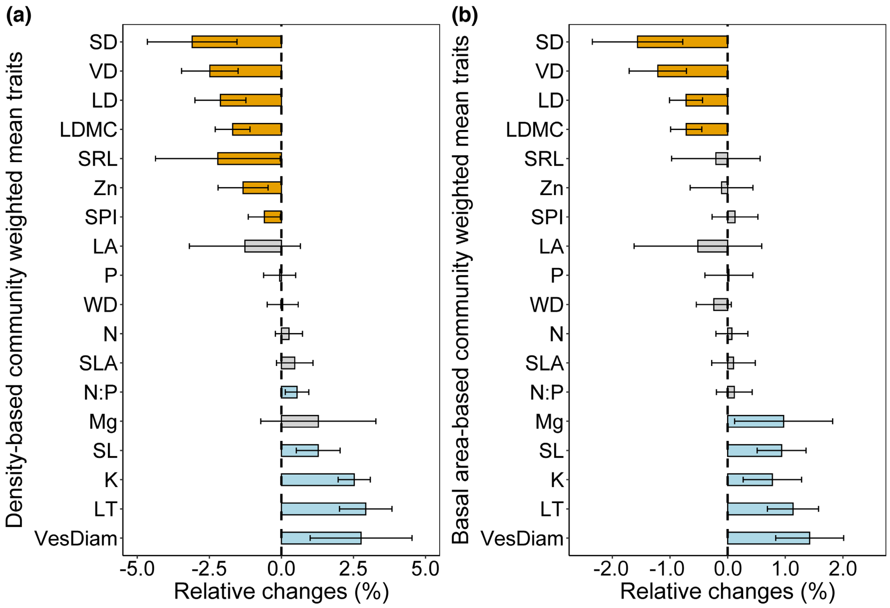

FIGURE 5 The relative change (Mean ± *95% confidence interval*) of 18 community-weighted mean (CWM) traits of liana communities over a 5-year period in 20 1-ha plots in Xishuangbanna tropical seasonal rain forest, SW China. CWM traits in panel (a) weighted by relative density, and in panel (b) weighted by relative basal area. The traits are ordered from decreasing towards increasing values. Significances are based on the *t*-test with orange bars indicating CWM traits showing a significant decrease, gray bars indicating no change, and blue bars indicating a significant increase. Eighteen traits were analyzed: leaf thickness (LT), leaf area (LA), specific leaf area (SLA), leaf dry matter content (LDMC), leaf density (LD), vein density (VD), stomatal density (SD), stomatal length (SL), stomatal pore index (SPI), leaf nutrient (N, P, K, Mg, and Zn) concentration, leaf N:P ratio (N:P), wood density (WD), vessel diameter (VesDiam), and specific root length (SRL).

between 2014 and 2019 (Figure S2b), for which we do not have a clear explanation. Yet, liana community changes may reflect lagged responses to past CO_2 increases. The liana communities became indeed more acquisitive in carbon and nutrient use (PC1). Increased water availability, or improved water use efficiency at high CO_2, may explain dynamics in liana communities (van der Sleen et al., 2015). First, it was the communities with slow water use (lower right quadrant of the PCA) that showed especially large increases in water use (PC2, i.e., SL) (Figure 5). Second, communities that had already fast water use (upper right quadrant) were especially able to show large increases in carbon use (PC1, Figure 5). Third, liana communities downregulated the capacity to capture water and soil nutrients, with lower SRL and leaf Zn and Mg concentration (PC2). From these observations, we hypothesize that CO_2 fertilization plays a critical role in the dynamics of this liana community, but we lack direct evidence for already drawing conclusions on this.

5 | CONCLUSIONS

It has been suggested that an increase in liana density and basal area is a general phenomenon for tropical forests (Phillips et al., 2002, Schnitzer & Bongers, 2011). Yet, several studies have shown that lianas are actually decreasing (e.g., Bongers et al., 2020; Gerolamo et al., 2018), suggesting that changes in lianas are context dependent (Bongers et al., 2020). We show that lianas decreased in density mainly because of the high mortality of smaller individuals but increased in basal area because of the high survival and growth of larger individuals. The liana community changed towards more, large, acquisitive lianas, which are particularly well suited for rapid water use. The trait shifts suggest that there was massive species turnover within the 5-year study period. There are more larger stems through time due to relatively low mortality of the larger individuals, which is associated with relatively low levels of disturbance. Our study shows how quantifying changes in abundance and functional traits of plant communities allows for comparing the possible roles of local and global drivers on plant community changes and emphasizes a strong role of local conditions for multi-annual changes in liana communities.

AUTHOR CONTRIBUTIONS

Q.L., F.J.S., J.L.Z., and L.P., conceived the ideas and designed the methodology; Q.L. collected the data, and performed the analyses with the help of L.P.; Q.L., F.J.S., J.L.Z., and L.P. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

All authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Species mean trait data are available from the TRY database. Data on liana density and basal area of each plot will be made available through Data Archiving and Networked Services (DANS): https://doi.org/10.17026/dans-2zd-fzdt.

ORCID

Qi Liu https://orcid.org/0000-0003-3962-0867

Frank J. Sterck https://orcid.org/0000-0001-7559-6572

Jiao-Lin Zhang https://orcid.org/0000-0003-3693-7965

Lourens Poorter https://orcid.org/0000-0003-1391-4875

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SUPPORTING INFORMATION

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