

Local dynamic variation of lianas along topography maintains unchanging abundance at the landscape scale in central Amazonia

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Abstract

Question: Have liana density and biomass increased in central Amazonia over the last 10 years? Can a spatially explicit consideration of liana mortality and recruitment rates across hydro-edaphic and tree turnover gradients at the landscape scale explain changes in liana density and biomass?

Location: Ducke Forest Reserve, 26 km north of Manaus, Amazonas, Brazil.

Methods: Data were collected on 30–1 ha permanent plots in a central Amazonia undisturbed old-growth rain forest 10 years after the first census. We measured lianas at 1.3 cm above their rooting point, with a diameter (D) ≥ 5 cm and subsampled lianas ≥ 1 cm diameter in 0.25 ha per plot. We estimated above-ground density and biomass changes, mortality rate, recruitment and diameter increase. Soil cations and available P were reduced to two dimensions with PCA and the first axis used as the descriptor of soil fertility. Height above the nearest drainage, a proxy for water availability, tree turnover ($D \geq 10$ cm) and soil fertility were used as predictors of liana dynamics.

Results: No significant change in liana density and biomass, averaged over the 30-km² landscape, was observed over the last 10 years. In 2014, liana density was generally higher in more fertile soils, and it increased in areas closer to the water table and with higher tree turnover in the valleys. This pattern resulted from the higher liana recruitment rates in valley plots closer to the water table. Liana mortality rates were uniform across plots, similar among the diameter classes and, on average, higher than recruitment.

Conclusion: We did not find any evidence that liana density and biomass have been increasing in this Neotropical site over the last 10 years. These findings suggest that the current knowledge on liana increase trends in the Neotropics should be reviewed if supported by further tropical studies.

KEY WORDS

above-ground biomass, central Amazonia, climbing ecology, liana mortality, liana recruitment, liana turnover, old-growth rain forest, tree turnover, vines



1 | INTRODUCTION

Lianas are key elements from which we can learn more about tropical forest dynamics, given their potential to affect trees and, hence, carbon balance (Schnitzer & Bongers, 2002, 2011). In the past few decades, an increase in liana density and biomass has been reported for several old-growth Neotropical forests (western Amazonia: Phillips et al., 2002; Foster, Townsend, & Zganjar, 2008; Guyana: Chave et al., 2008; Central America: Wright, Calderón, Hernández, & Paton, 2004; Ingwell, Joseph Wright, Becklund, Hubbell, & Schnitzer, 2010; Schnitzer et al., 2012; Yorke, Schnitzer, Mascaro, Letcher, & Carson, 2013; central Amazonia: Laurance et al., 2014). This change in liana density and biomass has been explained by at least four main hypotheses that can, directly or indirectly, operate simultaneously (Schnitzer & Bongers, 2011; Schnitzer, 2015). The first hypothesis attributes the increase in liana abundance to the increase in frequency and intensity of drought across the tropics, which, in turn, results from global climate change. This hypothesis is based on the fact that lianas were shown to assimilate more carbon and undergo less water stress than trees under dry conditions (Cai, Schnitzer, & Bongers, 2009). The second hypothesis suggests that the increase in CO₂ in the atmosphere enhances liana biomass and fecundity under certain ecological conditions (e.g., low luminosity and nutrient-poor environments), given their higher competitive capacity when compared to trees (e.g., Granados & Körner, 2002; Körner, 2009; however, see Marvin, Winter, Burnham, & Schnitzer, 2015). The third hypothesis holds that lianas have increased in abundance as a result of higher levels of natural disturbance due to increased rates of tree turnover. In this case, accelerated tree dynamics would benefit liana growth and establishment (Putz, 1984; Schnitzer & Carson, 2010). The fourth hypothesis posits that increased liana abundance can be explained by N deposition (Schnitzer, Bongers, & Wright, 2011), which is increasing in tropical forests (Hietz et al., 2011), and the ability of lianas to respond to this nutrient fertilization with more rapid growth (Schnitzer et al., 2011; Asner & Martin, 2015).

However, other studies showed a decline in liana density in the tropical forests of Africa (Caballé & Martin, 2001; Ewango, 2010; Thomas, Burnham, Chuyong, Kenfack, & Sainge, 2015; Bongers & Ewango, 2015) or no significant change in density in temperate US forests (Londré & Schnitzer, 2006). Although a pattern in liana density and biomass seems to be increasing in the Neotropical forest (Schnitzer, 2015), we know that global changes in climate or CO₂ levels over the last decades cannot explain an increase that is restricted to the Neotropics (Wright, Sun, Pickering, Fletcher, & Chen, 2015). In addition, it is possible that either the increase or decrease in lianas reported for some tropical sites is simply a local response to perturbations preceding those studies (Yorke et al., 2013; Bongers & Ewango, 2015). The low number of sites sampled in the Neotropics and the lack of consensus about the possible mechanisms underlying large-scale patterns reinforce the importance of new studies of lianas dynamics.

In the last years, an increase in liana density has been reported (ca. 1% year⁻¹ ha⁻¹) in central Amazonia (Laurance et al., 2014). This

area is located approximately 80 km north of Manaus (Amazonas, Brazil), the most populous city in the middle of the Amazon rain forest. Ducke Reserve, which has similar geomorphology and soils, is located approximately 30 km north of Manaus. Using a 10-year time frame, similar to that used by Laurance et al. (2014), we monitored this reserve with permanent plots, offering the unique opportunity to test the generality of those results and expand the studies dedicated to the liana dynamics, especially in Neotropical regions. Here, we evaluate liana density and biomass dynamics, mortality, recruitment and diameter increase in central Amazonia between 2004 and 2014. We investigate whether liana dynamics is associated with height above nearest drainage (HAND, a proxy for topography and soil hydrology), tree turnover and/or soil fertility, using a large set of plots systematically distributed on the central Amazonia landscape. Topography and soil hydrology have been shown to regulate several aspects of forest structure and dynamics (Clark & Clark, 1999; Costa, Magnusson, & Luizao, 2005; Castilho et al., 2006; Dalling et al., 2012), as well tree turnover and soil fertility (Schnitzer et al., 2011; Dalling et al., 2012) and might, therefore, be a local cause of variation in liana dynamics. We address the following specific questions: (a) have liana density and biomass increased in central Amazonia over the last 10 years; and (b) can a spatially explicit consideration of liana mortality and recruitment rates across a height above nearest drainage (HAND), tree turnover rate and soil fertility gradient explain changes in liana density and biomass at the landscape scale?

2 | METHODS

2.1 | Study site and plot distribution

Our study was carried out in the Adolpho Ducke Forest Reserve (hereinafter Ducke Reserve), which is managed by the National Institute of Amazonian Research (INPA), located 26 km north of Manaus (2°55'S, 59°59'W), in the State of Amazonas. The year-round mean monthly temperature is 26°C (Marques Filho, Dos Santos, & Dos Santos, 1981). The mean annual humidity is around 84% and the mean annual precipitation is 2,300 mm, with a rainy season from Oct to Jun and a dry season from Jul to Sept, when rainfall is generally <100 mm/month (Marques Filho et al., 1981). Ducke Reserve covers 10,000 ha (10 × 10 km) of the terra firme moist tropical forest, with a closed canopy 30- to 35-m tall, emergent trees up to 50-m high, and generally low light levels in the understorey (Guillaumet & Kahn, 1982; Ribeiro et al., 1999). The soils form a continuum from clayey latosols in the highest flat plateaus, with increasing sand on slopes, until turning into pure sand on valley bottoms (Chauvel, Lucas, & Boulet, 1987; Mertens, 2004).

Our liana inventory was conducted in 30 permanent plots systematically distributed across 30 km² of the reserve and spanning a range of altitudes from 39 to 140 m (Ribeiro et al., 1999; Figure 1). Each plot was 250-m long and 40-m wide, following the altitudinal contour (see Magnusson et al., 2005; Costa & Magnusson, 2010 for further design details), and separated from each other by at least

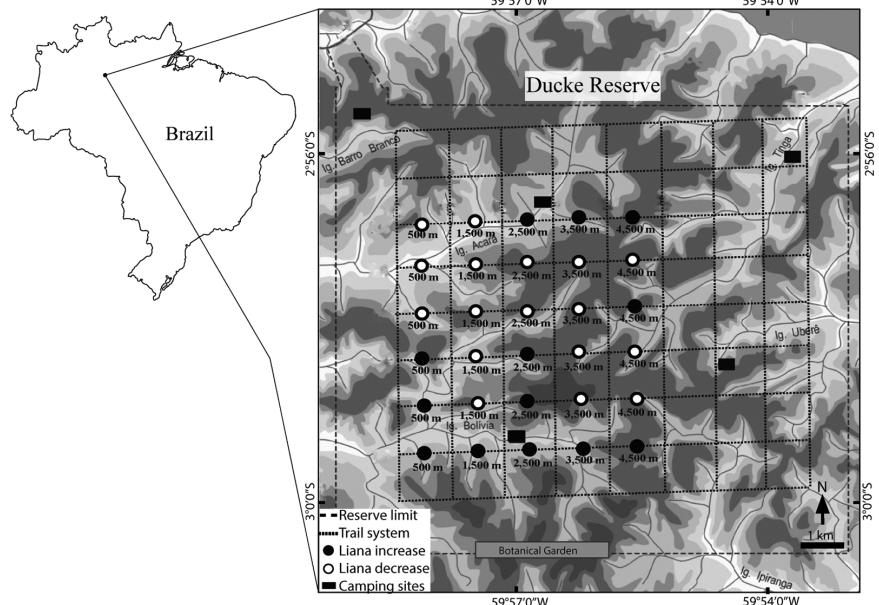


FIGURE 1 Map of the Ducke Reserve (Manaus, Brazil) showing the trail system and the position of the permanent monitoring plots (circles). Black circles represent liana increase, while white circles represent liana decrease. Grey shading shows topography, dark grey for high altitudes grading to white in the valleys (Adapted from Ribeiro et al., 1999)

1 km. This sampling design aimed to reduce internal variation in the hydro-edaphic features of each plot (Costa & Magnusson, 2010).

2.2 | Liana sampling

All lianas with diameter ($D \geq 5$ cm) were sampled in 1 ha/plot (250×40 m). Smaller lianas ($1 \text{ cm} \leq D \leq 4.9 \text{ cm}$) were subsampled within each plot in an area measuring 0.25 ha (250×10 m). We did not distinguish genetic individuals that might have been connected underground; instead, each stem was considered individually in the calculations. During a first census carried out between 2004 and 2005 (Nogueira, Costa, & Castilho, 2011) and second census carried out in 2014, we used identical methods: (a) marking all liana stems rooted within plots; (b) measuring the diameter at 1.3 m from the rooting point, following the stem contour; and (c) measuring the minimum and maximum diameter (S_{\min} and S_{\max}) of lianas with asymmetrical, non-cylindrical stems, as recommended by the protocol of Gerwing et al. (2006). We applied Equation 1 to obtain a corrected estimate of stem diameter (Gerwing et al., 2006).

$$D = \sqrt{S_{\min} \times S_{\max}} \quad (1)$$

2.3 | Descriptors of liana assemblage and temporal dynamics

For each plot and the overall landscape, we calculated liana density (stem/ha), dry biomass (kg/ha), annual rate of density change ($\text{stem ha}^{-1} \text{ year}^{-1}$), annual rate of biomass change ($\text{kg ha}^{-1} \text{ year}^{-1}$), mortality rate ($\% \text{ year}^{-1}$), recruitment rate ($\% \text{ year}^{-1}$), liana turnover ($\% \text{ year}^{-1}$) and periodic annual diameter increase (mm year^{-1}). For smaller lianas ($1 \text{ cm} \leq D \leq 4.9 \text{ cm}$) sampled within 0.25 ha, we standardized the descriptors for the 1-ha area of the plot to be comparable to large lianas sampled in the full 1 ha.

Liana density describes the number of liana stems per area (1 ha). Annual rate of density change was calculated by dividing

the difference in stem numbers between censuses by the exact time interval between censuses for each plot. To obtain the annual rate of biomass change, we initially estimated the above-ground dry biomass (AGBM) in kilograms, using allometric models described in Equation 2 (Schnitzer, DeWalt, & Chave, 2006), in which the diameter (D) used was 130 cm from the rooting point, as

$$\text{AGBM} = \exp[-1.484 + 2.657 \ln(D)] \quad (2)$$

The annual rate of biomass change was then calculated as the biomass difference between censuses divided by the time interval.

Annual mortality rate was calculated according to the logarithmic model of Sheil, Burslem, and Alder (1995), as

$$M = \{1 - [(1 - (N_0 - N_1)/N_0)^{1/\Delta t}]\} \times 100 \quad (3)$$

where M = annual mortality rate ($\% \text{ year}^{-1}$), N_0 = initial number of stems, and N_1 = number of stems surviving to time interval between censuses in years Δt .

Annual recruitment rate was calculated according to Nakagawa et al. (2000), as

$$R = \{[1 + (r/N_0)]^{1/\Delta t} - 1\} \times 100 \quad (4)$$

where R = annual recruitment rate ($\% \text{ year}^{-1}$), r = number of newly recruited stems, and N_0 = number of stems surviving to time interval between censuses in years Δt .

Liana turnover was calculated as the average of annual rates of liana mortality and recruitment (Phillips & Gentry, 1994).

Periodic annual diameter increase ($PI_{\text{diameter}} = \text{mm year}^{-1}$) was calculated as

$$PI_{\text{diameter}} = (D_f - D_i)/\Delta t \quad (5)$$

where D_f = final diameter, D_i = initial diameter, and Δt = timeframe.

All above descriptors were calculated for the diameter classes of 1.0–1.9 cm, 2.0–4.9 cm, 5.0–9.9 cm, 10.0–19.9 cm and ≥ 20 cm. Mortality and recruitment rates for lianas of $D \geq 20$ cm were not calculated since not enough stems were available for these classes (minimum of 20) at the first census, which would have inflated the mortality and recruitment rates (Lewis et al., 2004).

2.4 | Variation in HAND, soil fertility and tree turnover

In central Amazonia, several organisms, especially plants, change predictably in response to soil and topography (Costa, Guillaumet, Lima, & Pereira, 2009; Schietti et al., 2014); therefore, we used height above nearest drainage (HAND) and soil fertility to represent the hydro-edaphic gradient. HAND describes the vertical height of each plot in relation to the nearest drainage, which is an indirect estimate of the distance to the water table and can be derived from a Shuttle Radar Topography Mission (SRTM) digital elevation model (DEM; Rennó et al., 2008). Soil texture is highly correlated to HAND at Ducke Reserve; therefore, HAND incorporates both soil texture and hydrological aspects of the topography. High HAND values are associated with plots at high elevation and far from the water table, with clayey soils, while low HAND values represent plots in lowland areas closer to the water table, with sandy soils. Soil fertility was estimated with four variables (cmol kg^{-1}): K^+ , Ca^{2+} , Mg^{2+} and available P. In each plot, six superficial soil samples (0–5-cm deep) were collected at 50-m intervals, mixed into a composite sample, dried at 105°C , sieved (2 mm mesh size) and analysed at the INPA Soil Laboratory. A more detailed description of these variables is given in Castilho et al. (2006).

Additionally, lianas use trees as support to reach the canopy; therefore, changes in the dynamics of trees can correspondingly affect the dynamics of lianas (Schnitzer & Bongers, 2002). Thus, estimates of tree turnover per plot (the average of annualized rates of tree mortality and recruitment; Phillips & Gentry, 1994) were obtained from Castilho, Magnusson, de Araújo, and Luizão (2010), using the total number of dead and recruited trees with DBH > 10 cm over the course of 5 years (tree censuses undertaken between 2001 and 2005). These data were collected in the same permanent plots in which we sampled lianas for the present study. Because we do not have tree turnover data that precisely match the time frame of lianas, we assumed that tree turnover rate was constant during the liana sampling period.

2.5 | Statistical analyses

To estimate whether liana density and biomass had changed over the course of 10 years, we compared the averages of liana density and biomass between the two censuses: 2004–2005 (Nogueira et al., 2011) and 2014 (present work), using paired t-tests for each descriptor. We also performed these analyses per diameter size classes: 1.0–1.9 cm; 2.0–4.9 cm; 5.0–9.9; 10.0–19.9 and >20 cm. Since more thin than thick lianas were sampled, we chose to decompose the liana assemblage descriptors into unequal size classes, following

an approximate logarithmic distribution, similar to that applied by Nogueira et al. (2011). Change in liana recruitment, mortality, turnover and diameter increase among size classes were assessed with one-way analysis with permutation tests, followed by post-hoc analysis with pair-wise permutation tests for multiple comparisons ($p \leq 0.05$). We carried out LM to test the relationships between liana density and biomass in 2014, annual density and biomass change with annual recruitment, and mortality rates.

The HAND, tree turnover and soil fertility (concentration of Ca^{2+} , Mg^{2+} , K^+ and available P) were used to predict the variation of seven descriptors of structure and temporal dynamics of liana assemblage. We used PCA to reduce the dimensionality of the multiple soil descriptors, in which the first PCA axis (PC1) with variance >1 (Norusis, 1990) was used in subsequent analyses. Loadings of variables related to PC1 were used to describe the most important soil fertility descriptors (Supporting information Appendix S1). Due to the significant correlation between HAND and tree turnover ($r = -0.38$) and HAND and soil fertility ($r = 0.53$) (details in Supporting information Appendix S2), we constructed two different LM. We separately tested the relationship between liana dynamic descriptors and HAND (Model 1) and the relationship between liana dynamic descriptors and tree turnover plus soil fertility (Model 2). Normality and variance homogeneity were checked in all cases. All statistical analyses were performed in the R environment (v. 3.2.1; R Foundation for Statistical Computing, Vienna, AT). Permutation tests for linear models used the coin packages (Hothorn, Hornik, van de Wiel, & Zeileis, 2008).

3 | RESULTS

3.1 | Liana recruitment, mortality and diameter increase rates

The annual recruitment rate per hectare was $3.25 \pm 1.48\% \text{ year}^{-1}$, the annual mortality rate was $5.39 \pm 1.75\% \text{ year}^{-1}$ and the liana turnover was $4.32 \pm 1.12\% \text{ year}^{-1}$ (Table 1). Annual recruitment rate varied between diameter classes (Table 1; $Z = -3.319$, $df = 106$, $p < 0.001$) and was higher in the smaller diameter class (1.0–1.9 cm) when compared with other classes. Annual mortality rate was not significantly different among classes (Table 1; $Z = -0.81$, $df = 106$, $p = 0.41$). Liana turnover varied among diameter classes (Table 1; $Z = -2.08$, $df = 113$, $p = 0.003$) and was higher in the smallest diameter class (1.0–1.9 cm) when compared to the next higher classes, 2.0–4.9 cm and 5.0–9.9 cm.

Periodic mean annual diameter increase per hectare was $0.57 \pm 0.14 \text{ mm year}^{-1}$ and varied between diameter classes (Table 1; $Z = -2.75$, $df = 123$, $p = 0.005$). Lianas with stem diameter between 1.0 and 1.9 cm had the smallest periodic diameter increase at $0.18 \pm 0.05 \text{ mm year}^{-1}$. Lianas with stem diameters >20 cm had, on average, the highest increment ($4.7 \pm 2.56 \text{ mm year}^{-1}$).

3.2 | Liana dynamics at the landscape scale

We recorded 8,166 liana stems in the 30 permanent plots of Ducke Reserve in the census of 2004–2005, an average of

650 ± 272 stem/ha, and 8,122 stems in the same plots in 2014 with an average of 600 ± 252 stem/ha (Table 1). No significant change in liana density was observed between the two censuses at the landscape scale (over the 30 plots) for lianas with stems > 1 cm (Figure 2a; $t_{\text{paired}} = -1.80$, $df = 29$, $p = 0.08$).

The average biomass for lianas with stem diameters > 1 cm/ha was $4,596 \pm 1,578$ kg/ha in 2004–2005 and $4,930 \pm 1,727$ kg/ha in 2014. No significant change in liana biomass was detected between the two censuses at the landscape scale for stem diameters > 1 cm (Figure 2b; $t_{\text{paired}} = 1.82$, $df = 29$, $p = 0.07$).

3.3 | Liana dynamics across diameter size classes

The highest density of stems (~55%) was concentrated in the smaller size class (1.0–1.9 cm). On average, this class experienced the highest absolute reduction in density across censuses, from 389 to 330 stems/ha (Figure 3a; $t_{\text{paired}} = -2.67$, $df = 29$, $p = 0.012$), followed by size class 5.0–9.9 cm, with a reduction of 54–49 stems/ha (Figure 3a; $t_{\text{paired}} = -2.78$, $df = 29$, $p = 0.009$).

Liana biomass peaked in the intermediate diameter size class in both censuses ($5.0 \text{ cm} < D \leq 9.9 \text{ cm}$; Figure 3b). No significant change was observed in liana biomass within each size class between the two censuses (Figure 3b).

3.4 | Liana density and biomass dynamics at the local scale: recruitment and mortality

Locally, standing liana dry biomass in 2014 was not significantly associated with either recruitment or mortality rates (Table 2). On the other hand, the annual rate of biomass change was negatively correlated with mortality (Table 2); consequently, areas with higher mortality decreased in biomass.

3.5 | Liana density and biomass dynamics at the local scale: HAND, tree turnover and soil fertility

The first PCA axis explained 69% of the variation in the original data set and is an indicator of soil fertility, running from higher levels of

TABLE 1 Descriptive statistics (mean \pm SE) of liana dynamic descriptors per diameter size class ($n = 30$)

Descriptors	Unit	1.0–1.9 cm	2.0–4.9 cm	5.0–9.9 cm	10.0–19.9 cm	≥ 20 cm	Total
Recruitment rate	(% year $^{-1}$)	$3.84 (\pm 0.39)^a$	$2.70 (\pm 0.28)^b$	$2.29 (\pm 0.17)^b$	$2.40 (\pm 0.31)^b$	–	$3.25 (\pm 10.27)$
Mortality rate	(% year $^{-1}$)	$5.87 (\pm 0.38)^a$	$4.84 (\pm 0.35)^a$	$4.92 (\pm 0.41)^a$	$5.41 (\pm 0.52)^a$	–	$5.39 (\pm 0.32)$
Liana turnover	(% year $^{-1}$)	$4.85 (\pm 0.26)^a$	$3.77 (\pm 0.25)^b$	$3.60 (\pm 0.23)^b$	$4.04 (\pm 0.37)^{a,b}$	–	$4.07 (\pm 0.20)$
Diameter increase	(mm year $^{-1}$)	$0.19 (\pm 0.009)^a$	$0.53 (\pm 0.02)^b$	$0.83 (\pm 0.04)^c$	$1.80 (\pm 0.12)^d$	$4.7 (\pm 0.546)^e$	$0.57 (\pm 0.02)$

Note. Different letters in each line indicate differences among size classes, according to pair-wise Permutation test at 5%.

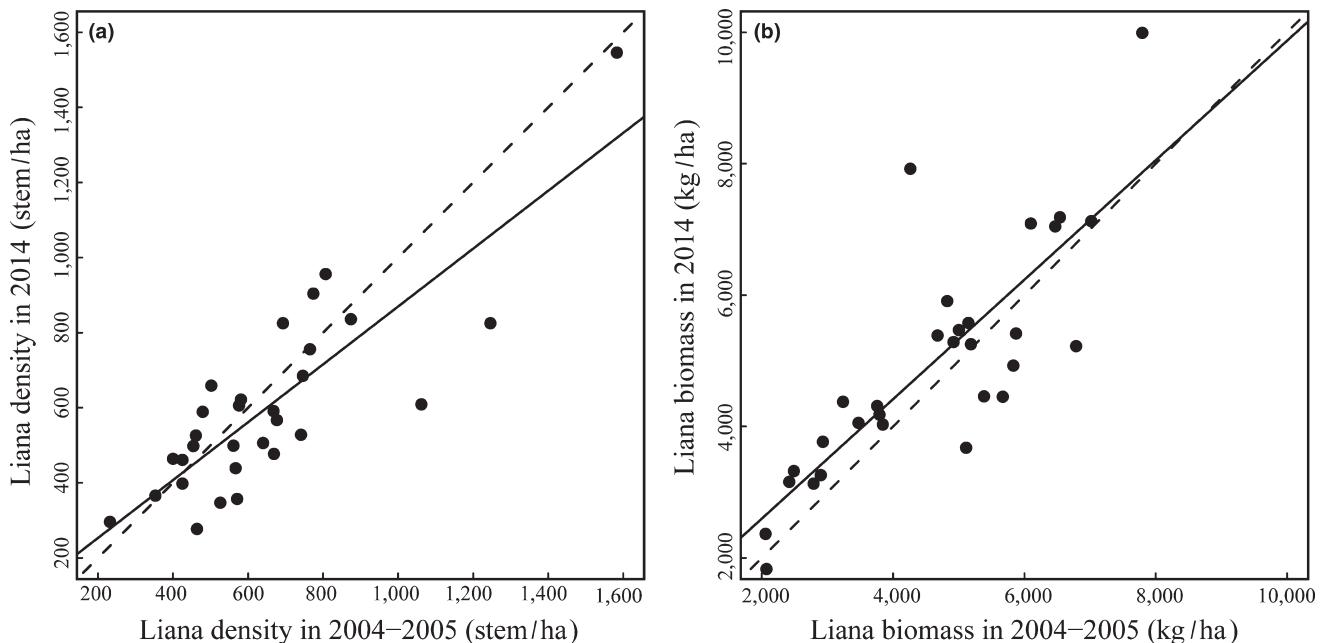


FIGURE 2 Comparison of liana density (a) and above-ground dry biomass (b) between the censuses of 2004–2005 and 2014 in 30 1-ha plots in central Amazonia (lianas with $D \geq 1$ cm). The dashed line represents the relationship of $Y = X$ in a scenario of zero change in liana density, while the continuous line is the linear regression of liana density between the two censuses

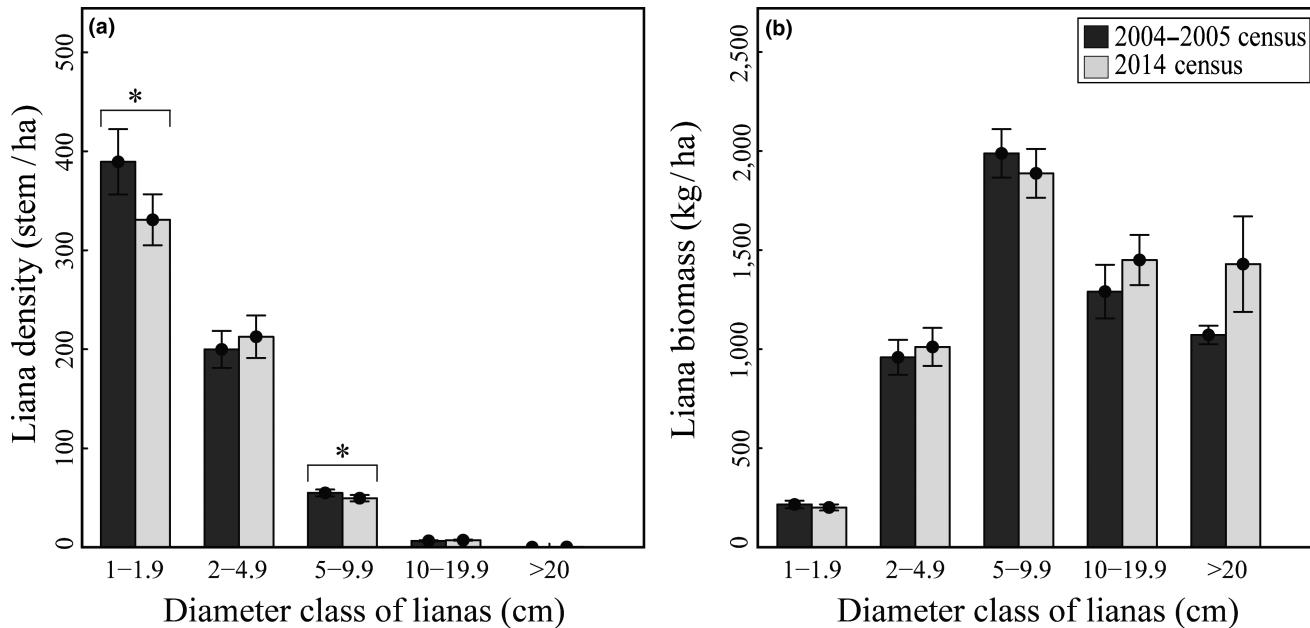


FIGURE 3 Mean (\pm SE) of liana density (a) and liana above-ground dry biomass (b) per diameter class in 30 1-ha plots in central Amazonia. In black, data from the first census (2004–2005, $n = 18.015$); in grey, data for the second census (2014, $n = 19.522$). Asterisk indicates significant differences between censuses, and in both cases, lower values were found in the 2014 census

Mg^{2+} , K^+ and Ca^{2+} (loading > 0.5) in the positive scores to higher values of available P (loading = 0.34) in the negative scores (Supporting information Appendix S1).

Liana density in 2014 was positively related to soil fertility ($PC_1, \beta_{st} = 0.40, df = 27, p = 0.03$; Table 3) in that it was higher in more fertile areas. The annual rate of density change was negatively related to HAND ($\beta_{st} = -0.43, df = 27, p = 0.04$) and positively related to tree turnover ($\beta_{st} = 0.39, df = 27, p = 0.03$), but it was not associated with soil fertility (Table 3). Positive density changes were associated with lower HAND areas closer to the water table and higher mean tree turnover (Figure 4a, b). Biomass in 2014 was positively related to HAND ($\beta_{st} = 0.45, df = 27, p = 0.03$; Figure 4c), but the annual rate of biomass change was not associated with HAND, tree turnover or soil fertility (Table 3).

The annual rate of recruitment was negatively related to HAND ($\beta_{st} = -0.57, df = 27, p = 0.007$), but not to the tree turnover or soil fertility (Table 3). Plots with higher recruitment rates were those with lower HAND (Figure 4d). Liana mortality rate and diameter increment did not significantly differ along HAND, tree turnover or soil fertility over the landscape (Table 3).

4 | DISCUSSION

Our study shows that lianas did not significantly increase or decrease in either density or biomass over the last 10 years across a forest landscape of 30 km² in central Amazonia. On a local scale, 44% of the plots experienced increases and 56% decreases in liana density, which, when considered together, cancel out at landscape scale, resulting on average in zero net

TABLE 2 Relationships between descriptors of liana assemblage and both annual liana recruitment and mortality rates

Response variable	Factor	Estimate (β_{st})	SE	t	p
Liana density 2014	Recruitment	0.02	0.17	0.13	0.89
	Mortality	-0.39	0.17	-2.24	0.03
Annual rate of density change	Recruitment	0.77	0.06	12.5	<0.001
	Mortality	-0.51	0.06	-8.37	<0.001
Liana biomass 2014	Recruitment	-0.005	0.19	-0.02	0.97
	Mortality	-0.14	0.19	-0.76	0.44
Annual rate of biomass change	Recruitment	0.02	0.16	0.16	0.89
	Mortality	-0.55	0.16	-3.42	0.001

Note. Standardized multiple linear regression coefficients (β_{st}) and significant coefficients ($p \leq 0.05$) are shown in bold ($n = 30$).

change. The density of lianas was higher in the most fertile plots, while biomass was higher in plots far from the water table. Local increases in liana density occurred in valley plots, closer to the water table, where tree turnover was higher, as well as liana recruitment. Local decreases in liana density occurred in plateau plots, further from the water table, where tree turnover was lower and liana recruitment was lower than mortality. The liana mortality and the annual diameter increase were distributed uniformly along the explored ecological gradients across in the landscape.

4.1 | Liana density does not change at the landscape scale

Some studies report that liana density and biomass have been increasing in Neotropical forests in past decades (Phillips et al., 2002; Chave et al., 2008; Schnitzer & Bongers, 2011; Enquist & Enquist, 2011; Schnitzer et al., 2012; Yorke et al., 2013). More recently, Laurance et al. (2014) reported increases in liana density in the Biological Dynamics of Forest Fragments Project (BDFFP), an area only 60 km from our study site. Both sites – BPDF and Ducke – have similar climate and vegetation type, but contrasting results. In fact,

we found, for the first time, that liana density has not increased over the course of 10 years in a Neotropical forest, even after adjusting for differences in the inclusion diameter of lianas per plot as the basis for comparison ($D \geq 2, 5$ or 10 cm; Supporting information Appendix S3).

Hypotheses to explain the increase of lianas in Neotropical forests suggest that the rise of forest disturbances, fertilization by increased atmospheric CO_2 or nutrient deposition, and seasonality intensification are the potential drivers of the observed changes (Schnitzer & Bongers, 2011; Schnitzer, 2015). However, while fertilization by either CO_2 or nutrients is increasing globally (Schnitzer, 2015), not all sampled sites have benefited from increased liana

TABLE 3 Relationships between descriptors of liana assemblage and potential predictors, including height above the nearest drainage (HAND) (Model 1) and soil fertility (PC1) plus tree turnover (Model 2)

Model	Response variable	Factor	Estimate (β_{st})	SE	t	p	Figure
1	Liana density 2014	HAND	0.30	0.18	1.67	0.10	-
2	Liana density 2014	Tree turnover	0.05	0.17	0.29	0.07	-
		Soil fertility (PC1)	0.40	0.17	2.23	0.03	-
1	Annual rate of density change	HAND	-0.36	0.17	-2.08	0.04	4a
2	Annual rate of density change	Tree turnover	0.39	0.17	2.22	0.03	4b
		Soil fertility (PC1)	-0.02	0.17	-0.16	0.87	-
1	Liana biomass 2014	HAND	0.36	0.17	2.10	0.04	4c
2	Liana biomass 2014	Tree turnover	-0.28	0.18	-1.50	0.14	-
		Soil fertility (PC1)	0.03	0.18	0.16	0.86	-
1	Annual rate of biomass change	HAND	0.05	0.18	0.30	0.27	-
2	Annual rate of biomass change	Tree turnover	0.18	0.18	1.01	0.32	-
		Soil fertility (PC1)	-0.23	0.18	-1.26	0.21	-
1	Liana recruitment rate	HAND	-0.41	0.17	2.40	0.02	4d
2	Liana recruitment rate	Tree turnover	0.33	0.18	1.79	0.08	-
		Soil fertility (PC1)	0.05	0.18	0.30	0.76	-
1	Liana mortality rate	HAND	-0.08	0.18	-0.42	0.67	-
2	Liana mortality rate	Tree turnover	-0.26	0.18	-1.42	0.16	-
		Soil fertility (PC1)	-0.006	0.18	-0.03	0.97	-
1	Liana diameter increase	HAND	-0.04	0.18	-0.22	0.82	-
2	Liana diameter increase	Tree turnover	-0.14	0.19	-0.72	0.47	-
		Soil fertility (PC1)	-0.03	0.19	-0.20	0.84	-

Note. Standardized multiple linear regression coefficients (β_{st}) and significant coefficients ($p \leq 0.05$) are shown in bold ($n = 30$).

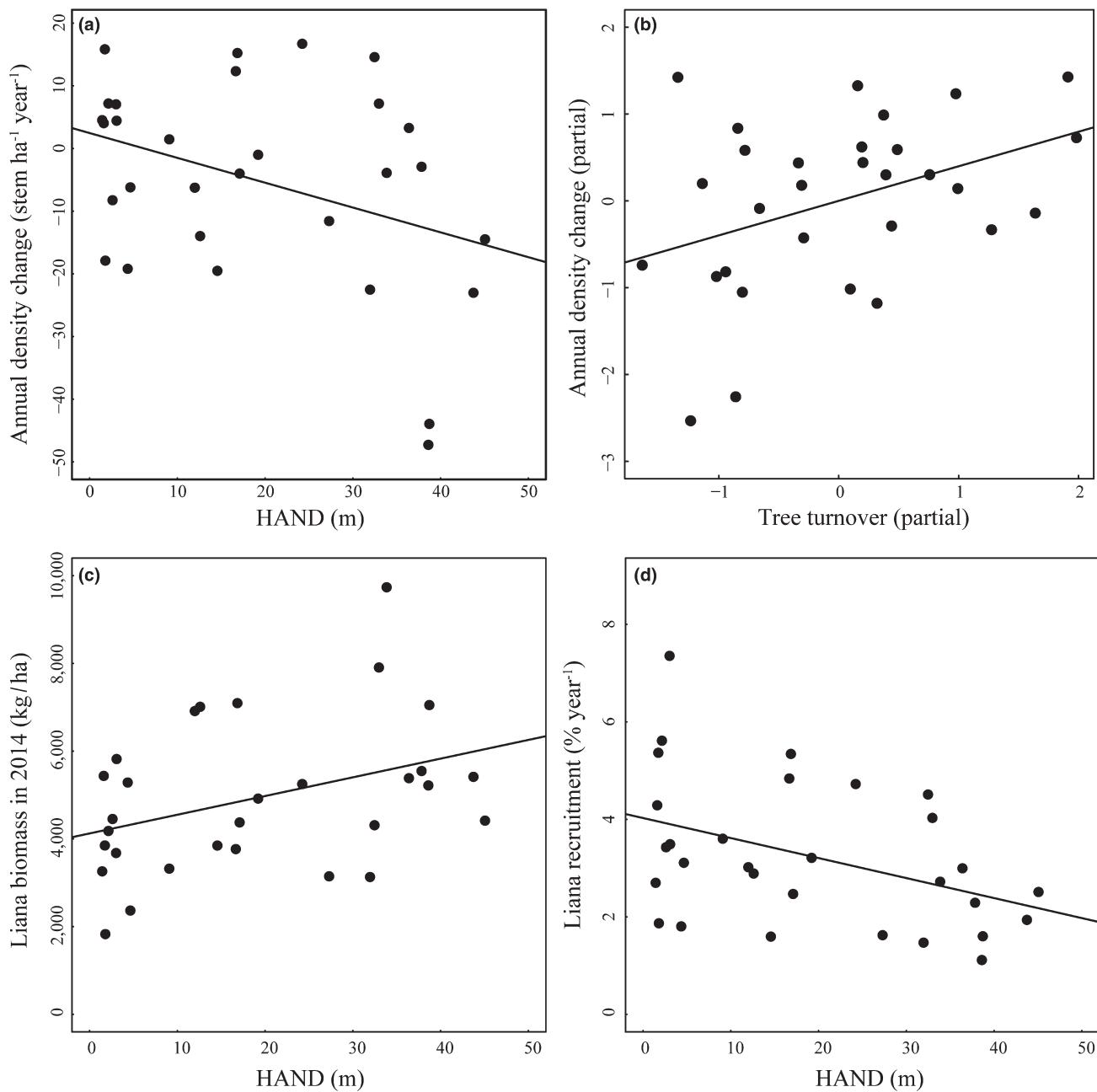


FIGURE 4 Relationships between liana assemblage descriptors: (a) Annual density change and height above the nearest drainage (HAND); (b) Annual density change and tree turnover; (c) Liana above-ground dry biomass and HAND; (d) Liana recruitment and HAND. Lines are shown only for significant relationships ($p \leq 0.05$)

abundance or biomass, including ours in the Neotropics. Therefore, it cannot be assumed that these factors are general drivers of change in liana abundance (Marvin et al., 2015; Wright et al., 2015). On the other hand, despite variation in the intensification of seasonality across the Neotropics (Malhi & Wright, 2004), it is similar on smaller spatial scales, such as that within central Amazonia, including both BDFFP and Ducke Reserve (Nogueira et al., 2015). Consequently, these global drivers cannot explain our results. Instead, differences between BDFFP and Ducke sites within central Amazonia suggest that locally varying factors, such as forest disturbances, may have been the cause of increases in liana abundance in BDFFP, while no

comparable changes occurred at Ducke Reserve. For example, the mean tree turnover rates in BDFFP (~1.3% year⁻¹; censuses undertaken between 1980 and 2009; Laurance et al., 2014) were higher than those at Ducke Reserve (~0.6 ± 0.28% year⁻¹; censuses undertaken between 2001 and 2005; Castilho et al. 2010). This could be explained by better light conditions at BDFFP, promoting liana growth and, hence, the increase in abundance.

In addition, increase in turnover rates may be a consequence of unknown past disturbances that could explain momentary increases or decreases in liana density (Yorke et al., 2013; Bongers & Ewango, 2015). Large disturbances, such as severe droughts or blowdowns



occurring before or at the beginning of the monitoring period, could lead to increases in liana density due to large recruitment in more favourable light conditions (Gentry, 1991). Therefore, the increase of lianas observed by Laurance et al. (2014) may be linked to major disturbances, such as blowdowns, which occur with more frequency as we move north from Manaus towards the BDFFP site (Espírito-Santo, Keller, Braswell, Nelson, & Frolking, 2010). In fact, strong windstorms and blowdowns were reported in central Amazonia in 2004 and 2005 (Espírito-Santo et al., 2014), and although they affected the entire region, very large blowdowns (≥ 30 ha; Nelson, Kapos, Adams, Oliveira, & Braun, 1994) were reported at BDFFP, while at Ducke Reserve, no blowdowns with the same magnitude was reported during the study periods, and windstorms mostly affected valleys (Toledo, Magnusson, Castilho, & Nascimento, 2012).

4.2 | Hydro-edaphic gradient and tree turnover determine liana dynamics

Higher densities and biomass of lianas were found in more fertile soils and plateau areas, respectively, where edaphic conditions may favour growth (Kazda & Mehlreter, 2001; Kazda, 2015) and long-term accumulation of stem and total liana biomass. However, along with the evaluated time frame, the increase in liana density in the valleys occurred where tree dynamics was accelerated and fostered liana recruitment. Uprooted trees account for a large fraction of tree mortality in the valleys due to soil instability (Castilho et al. 2010; Toledo, Magnusson, Castilho, & Nascimento, 2011; Toledo et al., 2012). Consequently, large gaps tend to be formed in these areas, which favour liana recruitment. Increase in liana density associated with higher tree turnover has been described for other tropical sites (Schnitzer et al., 2012; Laurance et al., 2014; Schnitzer, 2015), as well as increases associated with higher luminosity (Putz, 1984, 1990; DeWalt et al., 2015). Valley areas closer to the water table are also less susceptible to drought stress, and such areas are more conducive to higher sap flow, stomatal conductance and photosynthesis rates (Chen et al., 2015). The absence of water limitation in the valleys and higher light availability from accelerated tree turnover may have provided the ecological conditions required for faster growth and the observed higher recruitment of lianas.

4.3 | Methodological issues

Different sampling methodologies directly affect estimates of liana structure and diversity (Schnitzer et al., 2006; Schnitzer, 2015). Methodological decisions, such as diameter of inclusion and the point of measurement may lead to over- or underestimates of changes in density and biomass of lianas. Furthermore, plot size and spatial arrangement of sampling units at the landscape determine the patterns that can be recorded, since particular patterns emerge at different scales of investigation (Turner, Gardner, & O'Neill, 2001). Unobserved large-scale disturbance and disturbance caused by intense use of plots and trampling can also affect demographic estimates (Fisher, Hurtt, Thomas, & Chambers, 2008; Semboli, Beina, Closset-Kopp, Gourlet-Fleury, & Decocq, 2014) and need to be carefully controlled.

These aspects should be considered when comparing different studies. In the present study, we followed the recommended protocols for liana sampling (Gerwing et al., 2006), minimizing the potential effect of trampling on liana recruitment by preferentially using a single walkway along the plot during fieldwork. Plants in these walkways were not sampled. Our sampling scheme with plots distributed systematically in a large landscape (30 km^2) accounts for the environmental heterogeneity within the site, providing an unbiased geographic assessment of liana dynamics since, as we have shown here, these can vary locally in association with landscape features. This methodology (a) ensures that the absence of liana changes is not representative of sampling artifacts, and (b) suggests that a landscape perspective should be adopted more widely in studies of forest dynamics, as demographic rates are very sensitive to local environmental features.

5 | CONCLUSION

At the landscape scale, we observed that plot level positive and negative changes in liana density and biomass cancel each other out, resulting in zero net change over the 10-year period in the studied Neotropical forest. Liana mortality patterns were not related to environmental gradients and, thus, patterns of liana change resulted mainly from spatial differences in recruitment. Liana recruitment was favoured in valleys, which had higher tree turnover rates. Our results, combined with those of previous studies, suggest that global-scale factors are not universal drivers of liana changes in the Neotropics. At the landscape scale, the higher environmental heterogeneity within sites in the Neotropics, particularly that generated by edaphic-topographic and tree turnover variation, may play a major role in explaining liana dynamics. In addition, these findings suggest changes in the current knowledge on liana abundance increase trends in the Neotropics that can be supported by further studies.

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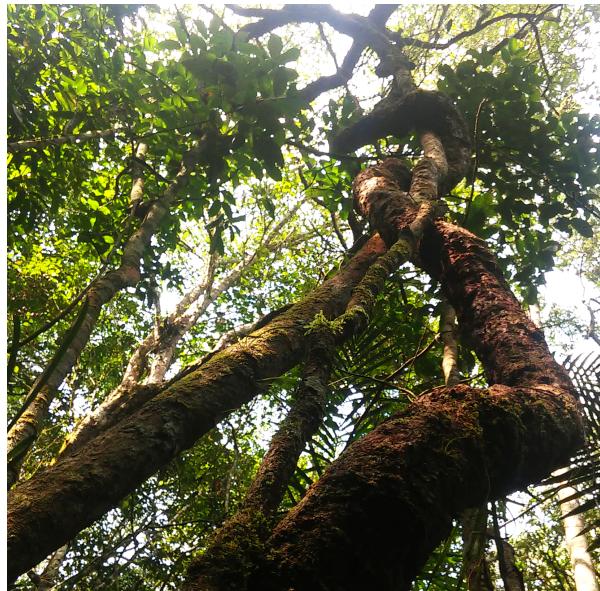
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Graphical Abstract

The contents of this page will be used as part of the graphical abstract of html only.
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We investigated the dynamics of liana density and biomass over 10 years in an undisturbed old-growth rainforest located in the central Amazon. To the best of our knowledge, this is the first study showing no evidence of liana increase in a Neotropical forest, highlighting the role of local disturbances linked to landscape topography in determining the variation of liana dynamics among plots.