RESEARCH ARTICLE

Long-term dynamics of liana seedlings suggest decelerating increases in liana relative abundance over time

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Abstract

1. Over the past decades, tropical forests have experienced both compositional and structural changes. In the Neotropics, researchers at multiple sites have observed significant increases in the abundance and biomass of lianas (i.e. woody vines) relative to trees. However, the role of dynamics at early life stages in contributing to increasing liana abundance remains unclear.

2. We took advantage of a unique dataset on seedling dynamics over 16 years in ~20 000 1-m^2 plots in a tropical forest in Panama to examine temporal and spatial trends in liana and tree seedling abundance.

3. We found that the relative abundance of liana seedlings increased across the study period, from 0.18 in 2001 to 0.24 in 2017. However, increases in liana seedling relative abundance appear to have levelled off in more recent years. The observed increases in liana relative abundance appear to be the result of both higher survival and higher recruitment rates of liana seedlings compared to tree seedlings.

4. Increasing liana abundance in the seedling layer was not explained by annual variation in dry season length, total rainfall or the proportion of area occupied by canopy gaps. In addition, liana seedlings did not exhibit a demographic advantage (i.e. higher recruitment or survival) over tree seedlings in dry habitats.

5. *Synthesis*. Our results reveal that seedling communities experienced important compositional changes in the past, but liana seedling relative abundance may have stabilized in recent years. Longer-term monitoring is needed to determine whether tropical forests will continue to experience compositional changes that may alter forest structure and ecosystem function.

KEYWORDS
Barro Colorado Island, forest structure, light gaps, Panama, precipitation, regeneration dynamics, topographic habitat

1 | INTRODUCTION

Lianas are important structural components of tropical forests, occupying about 50% of the canopy cover (Putz, 1984). During the last two decades, a number of studies have documented significant increases in the density and biomass of adult lianas in Neotropical forests (Phillips et al., 2002; Schnitzer & Bongers, 2011, but see, Smith, Queenborough, Alvia, Romero-Saltos, & Valencia, 2017), yet causes of this proliferation are largely unknown. The observed proliferation

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of adult lianas should also generate increases in lianas at earlier on-togenetic stages, such as higher production of liana seeds and higher liana seedling recruitment. Indeed, Umaña et al. (2019) reported an increase in the relative abundance of liana seedlings for a tropical forest in Puerto Rico from 2007 to 2017. In contrast, while Wright, Calderón, Hernandéz, & Paton, 2004 found increases in liana leaf litter production, liana seed production (over 14 years) and seedling proportion (over 8 years) fluctuated over time. If the same conditions that promote increases at the adult stage are also favourable for liana seedlings, we should see higher survival of liana seedlings over time and increasing relative abundance of liana species. However, compared to the recent spate of studies focused on increasing abundance of adult lianas, relatively little is known about changing dynamics of lianas at earlier ontogenetic stages. Examining changes in seedling community composition can provide insights into not only the processes underlying liana increases, but also whether increases in liana relative abundance will continue unabated into the future.

Increasing abundance of lianas in the seedling layer could result from either declines in seedling mortality rates, increases in seedling recruitment rates or both. Seedling recruitment is highly dependent on seed production, as well as on favourable conditions that allow the successful establishment of seedlings. Once established, seedling mortality is driven by biotic (e.g. pathogens, herbivores) and abiotic factors (e.g. limited light, moisture) that impair seedling performance (Augspurger, 1984; Clark & Clark, 1985; Johnson, Condit, Hubbell, & Comita, 2017; Uriarte, Muscarella, & Zimmerman, 2018). Demographic rates of both tree and liana species appear to be constrained by similar life-history trade-offs (between growth and survival rates) at the seedling stage (Gilbert, Wright, Muller-Landau, Kitajima, & Hernandéz, 2006). However, studies have also found key differences in liana versus tree responses to biotic and abiotic variables at early life stage (Muscarella et al., 2013; Umaña et al., 2019; Uriarte et al., 2018). For example, for seedling communities in a subtropical forest in Puerto Rico, lianas survived better than trees during drier years and in areas that experienced intense land-use history (Umaña et al., 2019; Uriarte et al., 2018). Thus, shifting conditions in tropical forests may differentially impact liana and tree seedling dynamics, leading to changes in the relative abundance of lianas in the understory. Such changes at the seedling stage are likely to influence later stages, since early life stages tend to be demographic bottlenecks and processes occurring at early stages play a significant role in shaping community composition and maintaining diversity in plant communities (Harper, 1977).

Multiple mechanisms have been hypothesized to explain observed increases in liana abundance (reviewed by Schnitzer & Bongers, 2011), several of which would likely influence recruitment and mortality at the seedling stage. First, Schnitzer (2005) suggested increasing liana abundance and biomass relative to trees could be due to increasing evapotranspirative demand (as a result of increased temperature and/or drought severity) because lianas are thought to have a demographic advantage (i.e. higher survival or recruitment) over trees under drier conditions. Previous studies on adult lianas have supported this hypothesis (Chen et al., 2015; van der Sande,

Poorter, Schnitzer, Engelbrecht, & Markesteijn, 2019; Swaine & Grace, 2007). Therefore, we would similarly expect liana seedlings to have a survival advantage over trees in drier habitats and in years with more severe droughts. An additional factor that could promote the proliferation of lianas is increased light availability due to disturbance (i.e. tree fall gaps) (Schnitzer, 2005, 2018). Previous studies have shown that canopy gaps and highly disturbed areas accumulate higher abundance and diversity of adult and seedling lianas (Dalling et al., 2012; Ledo & Schnitzer, 2014; Umaña et al., 2019). Thus, increases in the relative abundance of lianas may result from increases in the total area of canopy gaps within a forest.

We examined woody seedling dynamics across 16 years in a Neotropical lowland moist forest and compared liana and tree seedling dynamics, as well as changes in the relative abundance of these two growth forms over the study period. Using data on 396 species collected every 1–2 years between 2001 and 2017 in ~20,0000 1-m^2 seedling plots, we asked the following questions: (a) Are liana seedlings increasing in relative abundance in this tropical forest and are such changes constant over time? (b) Are observed changes in liana seedling relative abundance driven by lower mortality, higher recruitment or both? (c) Do liana seedlings outperform tree seedlings specifically in drier habitats, in drier years or in years that had a higher proportion of area open due to canopy gaps?

2 | MATERIALS AND METHODS

2.1 | Study site

The study was conducted on Barro Colorado Island (BCI), Panama (9°10′ N, 79°51′ W). The forest is classified as tropical moist forest according to Holdridge life-zones. Average annual temperature is 25.9°C, and average annual precipitation is 2,600 mm, the majority of which occurs during the wet season between May and December (Paton, 2016). During the study period, a strong ENSO event resulted in severe drought conditions during the 2015–2016 dry season. Between 1980 and 1982, a 50-ha permanent plot was established to monitor the dynamics of woody trees ≥1 cm diameter at 1.3 m above-ground (DBH) (Hubbell & Foster, 1983). The plot is predominantly old growth (>500 years), with a 2-ha area of secondary forest in the north-east corner of the plot. Although the island was affected in the past by anthropogenic activities, the old growth forest has not been cleared for agriculture in the last 1,500 years (Piperno, 1990).

2.2 | Seedling census

In 2001, a 1 × 1 m seedling plot was established in the centre of each 5 × 5 m subplot within the 50-ha plot, for a total of 20,000 plots used to monitor dynamics of early life stages. In the initial census in 2001, all free-standing woody individuals ≥20 cm tall and <1 cm DBH were tagged, identified to species and measured for height (Comita, Condit, & Hubbell, 2007). The seedling census included shrubs and trees (hereafter referred to simply as 'trees'),

but palm seedlings were excluded. Typically, lianas start life as free-standing seedlings in the forest understory before eventually using a host tree to climb for access to the canopy (but see Letcher & Chazdon, 2012). Liana seedlings were therefore included in the seedling census if they were ≥20 cm tall and not yet twining or climbing on other plants. Seedling plots were re-censused annually from 2002 to 2017, except for in 2005, 2007, 2010 and 2015 (for logistical reasons).

2.3 | Proportion of area in gaps

To assess light conditions in the understory, we used data from annual canopy censuses conducted between 2003 and 2012 (Hubbell, Comita, Lao, & Condit, 2014). In each year, for every 5 × 5 m quadrat within the 50-ha plot, the presence/absence of vegetation was recorded at different height classes: 0–1, 1–2, 2–5, 5–10, 10–20, 20–30 and >30 m above-ground. Using these data, we estimated the proportion of plot area with no vegetation (i.e. canopy gaps) above 1, 2 and 5 m for each year.

2.4 | Analyses

For our analyses, we used data on free-standing woody seedlings that were ≥20 and ≤100 cm tall, because taller liana seedlings usually start twining on other individuals (and thus were not captured by the seedling census).

We checked for temporal trends in liana versus tree seedling abundances in the BCI forest in several ways. First, we calculated the relative abundance of lianas in each seedling census (i.e. proportion of all woody seedlings that belonged to liana species) and plotted liana relative abundance over time. In addition, we calculated the population growth rate (λ) between 2001 and 2017 of liana and tree seedlings separately within each 1-ha quadrat (100 × 100m; 400 seedling plots per ha) of the 50-ha plot, using the formula: $(\lambda) = \frac{\ln n_t - \ln n_0}{\Delta t}$, where Δt is the census interval, n_t and n_0 are the population size at time t and time zero, respectively. We then tested for a difference between liana and tree seedlings in population growth rate using a paired t test after testing for normality using a Shapiro–Wilk test ($p > .05$).

To check whether the proportion of species exhibiting shifts in overall population growth rates was different between lianas and trees, we performed a chi-squared test in which we examined whether the portion of species that increased or decreased in abundance across the study period (2001–2017) was different between lianas and trees. For this test, we only used species with >20 individuals in the initial census to avoid any spurious effect caused by small changes in abundance of rare species.

To examine whether changes in population size were related to recruitment, mortality or both, we divided the dataset into four non-overlapping intervals, each three year long (2001–2004, 2006–2009, 2011–2014, 2014–2017), and calculated recruitment and mortality rates for lianas and trees separately in each 1-ha quadrat in each 3-yr interval. We calculated mortality (m) as $m = \frac{\ln n_0 - \ln S_t}{\Delta t}$, where the S_t is

the number of survivors at time t. We calculated recruitment (r) as $r = \frac{\ln n_t - \ln S_t}{\Delta t}$ (Hubbell, Condit, & Foster, 1990). Next, we performed a paired t test to examine differences between liana and tree seedlings in mortality or recruitment rates for each interval at each plot, correcting for multiple comparisons using the false discovery rate method (Benjamini & Hochberg, 1995).

To examine whether changes in the relative abundance of lianas over the study period were related to rainfall patterns, dry season length and/or light availability, we calculated the change in the relative abundance of lianas per census interval (Ch RA) and related it to annual precipitation (AP, mm), length of the dry season (LDS, days) and proportion of area in gaps (PG). We used a single model to test the effect of AP and LDS, and a separate model to test the effects of PG because data on gap area were only available for 2003–2012. For models of gap area effects, we ran separate models using gap area above 1, 2 and 5 m. However, results were qualitatively similar for all height cut-offs, and so we only present results using area of gaps above 1 m. Because community-level responses to abiotic variables do not occur instantaneously, we compared the change in the relative abundance of lianas to abiotic data from the previous year (e.g. the change in the relative abundance between 2008 and 2009 was linked to data on annual rainfall, dry season length and gap area from 2007). For the four census intervals that were two years long, we used the average abiotic information for the years prior to each year in the interval (e.g. for the interval 2014–16, annual rainfall was averaged for 2013 and 2014). In addition, we calculated the change in proportion of recruits and change in proportion of survivors per census interval and fit the same models. To examine changes in raw abundances of liana versus tree seedlings in response to the abiotic variables, we also ran similar models but instead of using the change in the relative abundance of lianas we calculated the change in absolute (log-transformed) abundance of liana and tree seedlings per census interval (Ch AB). The models had the following form: $\text{Ch AB} \sim \beta_0 + \beta_1 \times \text{GF} \times \text{AB}$. GF refers to growth form (i.e. liana or tree), and AB refers to the abiotic variable (i.e. either AP, LDS or PG).

To examine whether liana seedlings were better able to tolerate drier habitats compared to tree seedlings, we used the habitat classification of Harms, Condit, Hubbell, and Foster (2001), which assigned each 20 × 20 m subplot in the BCI 50-ha plot to one of seven habitat types: high plateau, low plateau, slope, stream, swamp, young (secondary forest) or mixed (i.e. more than one habitat type). For our analyses, subplots classified as *high plateau* and *low plateau* were assigned as "dry" habitats and *slope* and *stream* subplots were assigned as "wet" habitats, based on their soil moisture availability (Becker, Rabenold, Idol, & Smith, 1988; Comita & Engelbrecht, 2009, 2014; Grandgirard, Poinsot, Krespi, Nénon, & Cortesero, 2002). Previous studies have found effects of these habitat types on plant community composition, species distributions and tree seedling survival in the BCI 50-ha plot (Comita & Engelbrecht, 2009, 2014; Engelbrecht et al., 2007; Murphy, Salpeter, & Comita, 2016). *Swamp*, *Mixed* and *Young* habitat types were removed from the analyses because of their low representation in the 50-ha plot. We then examined the differences in mortality rates (from 2001 to 2017) between

lianas and trees per 20 × 20 m subplot as a function of habitat, life-form and the interaction of both using a linear mixed-effects model. Subplot was included as a random effect. The linear mixed model was conducted by using the "lmer" function from the package "lme4" in R (Bates, Mächler, Bolker, & Walker, 2015).

All analyses were performed in R version 3.4.4 (R Development Core Team, 2017).

3 | RESULTS

Between 2001 and 2017, 37,445 liana seedlings of 151 species and 139,835 tree seedlings of 2575 species (including morphospecies) were tagged and monitored in the seedling census. Liana seedlings increased in the relative abundance over the study period (Figure 1a), and the population growth rate of liana seedlings was significantly higher than tree seedlings between 2001 and 2017 (t = 7.7, p < .001, Figure S1). Increases in liana relative abundance were steepest in the first few years of the study (2001–2003) and continued to increase until 2014 when the values levelled off (Figure 1a). Changes in absolute abundance over time were similar for liana and tree seedlings, with both groups showing increases in seedling numbers between 2002 and 2008, and then a pronounced decline between 2008 and 2016, before a small uptick between 2016 and 2017 (Figure 1b). Despite the similarity in temporal trends in absolute abundance, increases were greater and declines were less for liana seedlings compared to tree seedlings, leading to increasing liana relative abundance in the seedling layer over the study period. We also found that the proportion of species that increased in seedling abundance was greater for liana species compared to tree species (chi-squared test, χ^2 = 3.92, p = .04) (Figure S2).

Liana seedlings had significantly lower mortality and higher recruitment rates compared to tree seedlings for intervals 1 and 2, but not for intervals 3 and 4 (Figure 2).

Graphs of annual variation in total rainfall, dry season length and proportion of area in gap clearly show that temporal trends in these abiotic factors do not mirror the observed increases over time in liana seedling abundance during the study period (Figure 1c–e). Consistent with this, none of these abiotic variables had significant effects in models of changes in liana relative abundance or in models of changes in absolute abundances of tree and liana seedlings (Table 1). Results comparing the effect of habitat type between lianas and trees showed no significant effect of habitat on mortality or recruitment, nor any significant interaction between habitat and growth form (Figure 3 and Table S1).

4 | DISCUSSION

Using our extensive, long-term data on tropical seedling dynamics, we found that the relative abundance of lianas in the seedling layer increased in the BCI forest dynamics plot over the 16-year period spanning 2001–2017. This pattern does not appear to be driven by one or a handful of species, but rather reflects a more general trend at the community level (Figure S2). The proliferation of lianas appears to be driven by both higher survival and higher recruitment of lianas compared to trees, particularly in the first eight years of the study. Higher recruitment could reflect a past increase in liana seed production, while both higher recruitment and survival likely reflect a potential physiological advantage that allows liana seedlings to establish and survive better than tree seedlings (van der Sande et al., 2019). Despite the hypothesized effects of water availability and canopy gaps in driving the increasing prevalence of lianas, we did not find differences in demography between liana and tree seedlings related to habitat type, nor any relationship between changes in liana seedling relative abundance and annual rainfall, dry season length or proportion of area in gaps. Overall, our results indicate that the seedling layer is mirroring patterns found for adult stages in other Neotropical forests (Phillips et al., 2002; Schnitzer & Bongers, 2011), where lianas have been shown to be increasing in the relative abundance compared to trees. Interestingly, however, our results show that these increases in liana seedling relative abundance appear to have levelled off in recent years, suggesting that there may be some limit to the increases in liana abundance observed in Neotropical forests. These results have important implications for understanding and predicting future changes in forest structure, species composition and carbon balance.

Our finding of increasing abundance of lianas over trees in the seedling layer agrees with a recently published long-term study from Puerto Rico that showed higher increases in liana seedling abundance relative to trees over a 10-year period (Umaña et al., 2019). However, additional studies focused on the seedlings stage are needed to determine whether this pattern extends to other tropical forests. Even within a single forest, temporal patterns of liana relative abundance may depend both on the time period and size classes examined. For example, a previous study at our study site in Panama showed more variable patterns in the proportion of liana seedlings during an earlier time period (i.e. 1994–2002) (Wright et al., 2004). That study by Wright et al. (2004) included seedlings smaller than our minimum size cut-off (20 cm tall). Younger seedlings tend to fluctuate more in abundance than older, established seedlings given that their dynamics are highly determined by seed production pulses followed by high mortality rates of seeds and young seedlings.

Our results also indicate that rates of liana proliferation varied over time. During the first nine years of our study, both lianas and trees increased in absolute abundance, with lianas showing higher rates of increase than trees; however, after 2008, the seedling community, both lianas and trees, experienced substantial declines. The most striking differences between liana and tree seedling dynamics during the first part of the study were the result of lower mortality and higher recruitment rates of lianas compared to trees during the first two intervals examined (2001–2004, 2006–2009). However, the rate of increase in liana relative abundance tended to decelerate over the later years of the study (Figure 1a), and the differences in demographic rates between lianas and trees were not significant in later census intervals (Figure 2). Observed
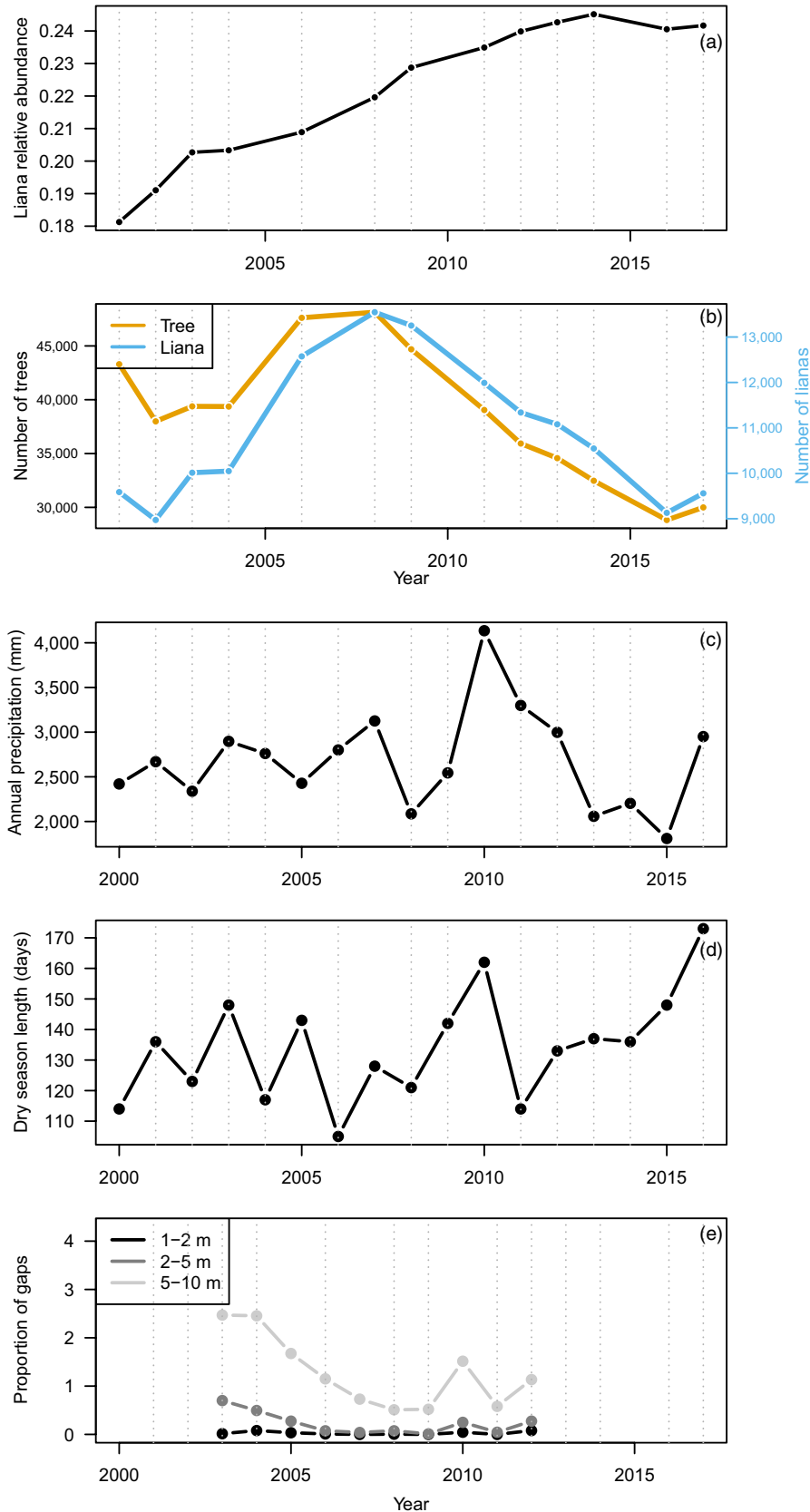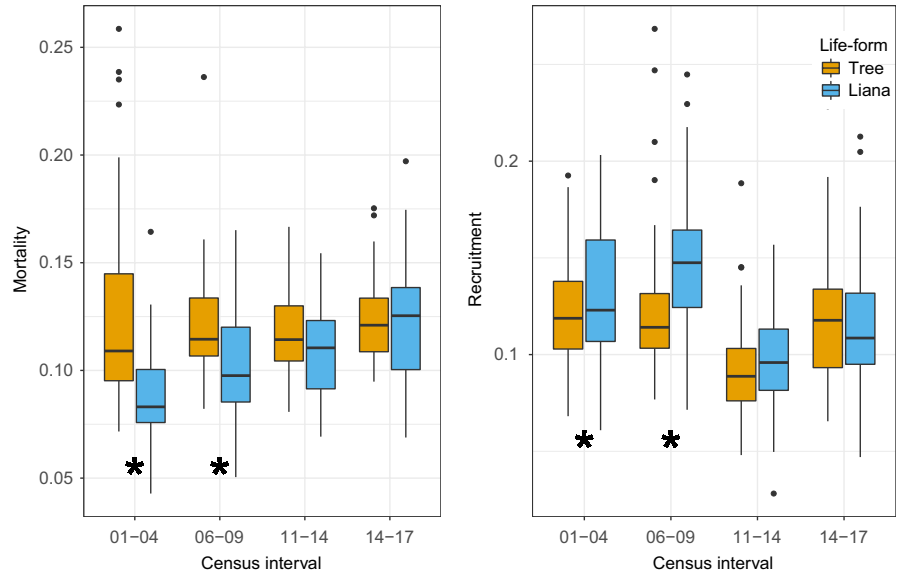
FIGURE 1 Temporal variation in the seedling community, precipitation and proportion of area in gaps in Barro Colorado Island (BCI), Panama. Plot (a) shows shifts in the relative abundance of lianas during the study period at 50-ha forest plot. Plot (b) shows shifts in liana and tree seedling numbers in the 50-ha plot seedling census. Plot (c) shows total yearly rainfall, and plot (d) shows length of the dry season for the period between 2000 and 2016. Plot (e) shows proportion of area in gaps for the period between 2003 and 2012. The dashed vertical lines indicate the years where seedling censuses were conducted. Note that y-axes do not include zero for plots (a–d) [Colour figure can be viewed at wileyonlinelibrary.com]

temporal trends in demographic success of liana seedlings have been attributed to variation in precipitation, which has shown significant relationships with liana seedlings dynamics in previous studies in Neotropical forests (Umaña et al., 2019; Wright et al., 2004). In particular, lianas are hypothesized to benefit over trees when water is limited because of special physiological

characteristics, such as good stomatal control, that allow them to exploit water more efficiently (Schnitzer, 2005). However, in our study, dry season length and total annual rainfall on BCI during the 16-year study period were not significantly related to shifts in the relative abundance of liana seedlings in the BCI forest or proportion of liana recruits or survivors (Table 1). We may have failed to detect trends related to annual climate fluctuations because four of the 12 census intervals included in our study spanned two years rather than one, and multiyear census intervals can obscure climatic signals in forest dynamics (Clark & Clark, 2011). However, visual inspection of annual variation in rainfall and dry season length (Figure 1c,d) suggests that it is unlikely that these variables explain the trend of increasing liana relative abundance over the course of the study. In addition, our study spanned a severe El Niño event in 2015–2016 that resulted in a particularly long dry season in 2016. However, liana seedling relative abundance showed only a small increase from 2016 to 2017, especially compared to the much larger increases in liana relative abundance observed earlier in the study in years with shorter dry seasons (Figure 1a). Thus, while several studies have shown that lianas have physiological advantages over trees under dry conditions (van der Sande et al., 2019), we found no evidence that lianas benefited over trees in dry years, at least at the seedling stage. However, we cannot rule out the possibility that increasing liana seedling relative abundance is a result of combined, interactive effects of multiple climatic variables (e.g. drought severity and night-time temperature). We also examined the potential positive effects of proportion of area in gaps on shifts in liana seedling abundance, but found no significant effect (Table 1). A potential explanation for this null result is that the study site is a relatively well-preserved forest that is not subject to frequent severe disturbances (e.g. hurricanes), and thus has a low proportion of disturbed areas at any given time (at the height of 1 m, the average proportion of area in gaps from 2003 to 2012 was 0.003; Table S2). Interestingly, the proportion of area in

gaps above 2 and 5 m was particularly high initially (i.e. 2003 and 2004) and then declined (Figure 1e). These areas with gaps above 2 or 5 m are likely older gaps that are beginning to fill in. Thus, we cannot rule out the possibility that the initial steep increases in liana relative abundance we observed were partly due to a delayed response to higher gap formation in the years just prior to the start of the seedling census, perhaps due to increased seed production of adult lianas leading to higher liana seedling recruitment. Future studies examining canopy gap dynamics prior to 2003, as well as spatially explicit analyses of liana seedling dynamics in gap versus non-gap areas of the 50-ha plot, would shed light on the potential role of canopy gaps in driving liana proliferation.

At regional scales, liana abundance has been shown to increase markedly with decreasing precipitation, increasing seasonality, and in soils with low water-holding capacity (Manzané-Pinzón, Goldstein, & Schnitzer, 2018; Swaine & Grace, 2007), leading to the hypothesis that lianas have a competitive advantage in drier, more seasonal environments and will increase in abundance with higher evapotranspirative demand (Schnitzer, 2005; Schnitzer & Bongers, 2011). We tested for a demographic advantage of lianas over trees under drier conditions by examining differences in mortality and recruitment between lianas and trees in topographic habitat types that differ in water availability (Condit, 1998; Hubbell & Foster, 1983). This topographic variation in soil moisture in the BCI plot drives significant habitat associations for both tree and liana species at the adult stage (Dalling et al., 2012). At the seedling stage, variation in water availability across these habitats has been shown to drive interspecific differences in tree seedling survival across habitats in the BCI forest (Comita & Engelbrecht, 2009). However, we found that tree and liana seedlings did not differ in mortality or recruitment responses to habitat. Thus, our results suggest that drier habitats do not favour lianas over trees at the seedling stage in this forest, although we cannot rule out differential responses to water availability at later life stages. Indeed, Dalling et al. (2012) found a high abundance of

TABLE 1 Coefficients of total annual rainfall, length of dry season and proportion of area in gaps from models of annual changes in (1) the relative abundance of lianas (2) proportion of liana recruits, (3) proportion of liana survivors, and from models of (4) log-transformed (raw) abundances of liana and tree seedlings per census interval in the BCI forest

Dependent variable		Estimate	Std. Error	t value	p value
Change in the relative abundance of lianas	(Intercept)	0.01	0.01	1.24	.25
	Total rainfall	3.5E-06	2.7E-06	1.26	.24
	Length dry season	−1.5E-04	7.7E-05	−1.90	.09
	(Intercept)	0.01	1.7E-03	3.33	.02
	Gap area	−0.04	0.05	−0.87	.43
Change in proportion of liana recruits	(Intercept)	9.65E-03	1.17E-02	0.82	.44
	Total rainfall	4.23E-06	2.70E-06	1.57	.16
	Length dry season	−1.24E-04	7.55E-05	−1.65	.14
	(Intercept)	0.008	0.002	3.68	.01
	Gap area	−0.093	0.060	−1.55	.18
Change in the proportion of liana survivors	(Intercept)	0.12	7.37E-02	1.66	.14
	Total rainfall	−9.85E-06	1.64E-05	−0.60	.57
	Length dry season	−6.71E-04	4.58E-04	−1.47	.19
	(Intercept)	0.01	0.01	0.99	.37
	Gap area	−0.23	0.38	−0.60	.57
Change in log-transformed abundance	(Intercept)	0.01	0.16	0.04	.97
	Liana	−0.02	0.23	−0.08	.94
	Total rainfall	−1.4E-05	5.9E-05	−0.24	.81
	Liana:Total rainfall	1.9E-05	8.4E-05	0.23	.82
	(Intercept)	−0.02	0.22	−0.07	.95
	Liana	0.16	0.32	0.51	.61
	Length dry season	−1.3E-04	1.6E-03	−0.08	.94
	Liana:Length dry season	−9.6E-04	2.3E-03	−0.41	.68
	(Intercept)	−0.02	0.05	−0.41	.69
	Liana	0.04	0.07	0.56	.59
	Gap area	−0.22	1.38	−0.16	.88
	Liana:Gap area	6.9E-04	1.95	0.03	.97

Note: Data on total rainfall and dry season length were available for all census intervals. Information on proportion of area in gaps was only available for the period between 2003 and 2012.
Abbreviation: BCI, Barro Colorado Island.

adult lianas in drier plateau habitats relative to wetter slope habitats in the BCI plot.

Increasing liana relative abundance has also been attributed to differences in dispersal strategy in the Neotropics: lianas tend to be dispersed by abiotic means (e.g. wind), while a larger proportion of tree species rely on animal dispersers, which have suffered large declines in many tropical forests (Wright, Hernandéz, & Condit, 2007; Wright, Sun, Pickering, Fletcher, & Chen, 2015). However, hunting is not permitted on BCI, and the forest there is well protected from poachers by park guards (Wright et al., 2007). Although bird inventories on BCI have found population decreases and in some cases complete extinctions, the guilds that experienced more pronounced declines were nectarivores and insectivores (Karr, 1982). Therefore, the seed disperser community appears to be largely intact on BCI, which has likely contributed to maintaining effective dispersion for

tree species dependent on animals (Jansen et al., 2012). Consistent with this, shifts in abundances of liana and tree seedlings between 2001 and 2017 were unrelated to species' dispersal strategy (Table S3). The observed increases in liana seedling relative abundance over time, despite the intact seed disperser community, indicate that other factors must have promoted the success of liana over tree seedlings in the BCI forest across our study period.

In conclusion, we show that the BCI seedling community experienced substantial increases in the relative abundance of lianas over a 16-year period. These increases were driven by both lower seedling mortality and higher recruitment of lianas compared to trees, but do not appear to result from differences between the growth forms in response to water or light availability. Although these two mechanisms cannot be ruled out at larger geographical scales, at the local scale, in our study, their effect on seedling community dynamics
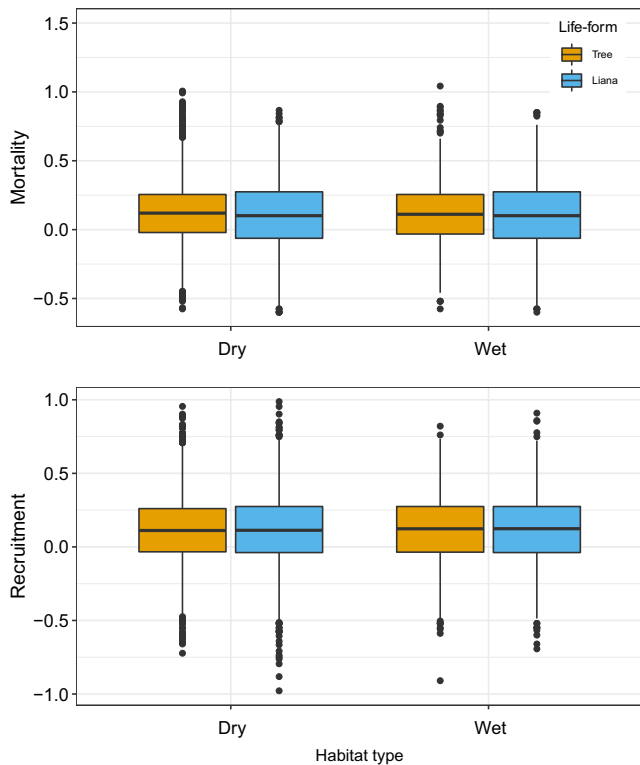
appears to be negligible. These results have implications for forest dynamics in the short run and long run, where the observed shifts not only imply changes in structure and composition of current seedling communities, but also indicate potential shifts in the carbon dynamics of the forest as well as arrested succession in disturbed areas that are dominated by lianas. Previous studies have shown that proliferation of adult lianas in tropical forests reduces forest-level carbon uptake and storage capacities (Durán, Gianoli, & Dura, 2013; van der Heijden, Powers, & Schnitzer, 2015). Observed changes in the seedling layer may be counteracted by processes at later life stages. However, if observed dynamics of earlier stages reflect dynamics of the future adult layer, tropical forests will likely face substantial alteration in their carbon dynamics. At the same time, our study also demonstrates that the increase in liana relative abundance in the seedling layer has levelled off in recent years. Whether increases in adult liana abundance and biomass in Neotropical forests will follow a similar trend remains to be seen. Continued long-term monitoring of tropical forests is needed to understand and predict how these ecologically and economically valuable ecosystems will be altered in a changing world.

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AUTHORS' CONTRIBUTIONS

M.N.U., E.M.-P. and L.S.C. designed the study. E.M.-P. and L.S.C. collected the data. M.N.U. analysed the data. M.N.U., E.M.-P. and L.S.C. wrote the manuscript.

DATA AVAILABILITY STATEMENT

Seedling census data are available from Dryad Digital Repository: https://doi.org/10.5061/dryad.k3j9kd53k for years 2001–2017 (Umaña, Manzané-Pinzón, & Comita, 2019). Canopy census data are available from https://repository.si.edu/handle/10088/21929, and climate data are available from https://biogeodb.stri.si.edu/physical_monitoring/research/barrocolorado.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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