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LETTER

Local canopy disturbance as an explanation for long-term increases in liana abundance

Stefan A. Schnitzer^{1,2}  | David M. DeFilippis¹  | Marco Visser³  |
 Sergio Estrada-Villegas^{1,2,4}  | Rigoberto Rivera-Camaña¹ | Boris Bernal¹ |
 Salomé Pérez¹ | Abelino Valdéz¹ | Seberino Valdéz¹ | Antonio Aguilar¹ |
 James W. Dalling^{2,5}  | Eben N. Broadbent⁶  | Angelica M. Almeyda Zambrano⁷  |
 Stephen P. Hubbell^{2,8}  | Maria Garcia-Leon¹

¹Department of Biological Sciences, Marquette University, Milwaukee, Wisconsin, USA

²Smithsonian Tropical Research Institute, Balboa, Panamá

³Institute of Environmental Sciences, Leiden University, Leiden, The Netherlands

⁴Yale School of the Environment, Yale University, New Haven, Connecticut, USA

⁵Department of Plant Biology, University of Illinois, Urbana, Illinois, USA

⁶School of Forest Resources and Conservation, University of Florida, Gainesville, Florida, USA

⁷Center for Latin American Studies, University of Florida, Gainesville, Florida, USA

⁸Department of Ecology and Evolutionary Biology, University of California – Los Angeles, Los Angeles, California, USA

Correspondence

Stefan A. Schnitzer, Department of Biological Sciences, Marquette University, PO Box 1881, Milwaukee, WI 53201, USA. Email: S1@mu.edu

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Abstract

Canopy disturbance explains liana abundance and distribution within tropical forests and thus may also explain the widespread pattern of increasing liana abundance; however, this hypothesis remains untested. We used a 10-year study (2007–2017) of 117,100 rooted lianas in an old-growth Panamanian forest to test whether local canopy disturbance explains increasing liana abundance. We found that liana density increased 29.2% and basal area 12.5%. The vast majority of these increases were associated with clonal stem proliferation following canopy disturbance, particularly in liana-dense, low-canopy gaps, which had far greater liana increases than did undisturbed forest. Lianas may be ecological niche constructors, arresting tree regeneration in gaps and thus creating a high-light environment that favours sustained liana proliferation. Our findings demonstrate that liana abundance is increasing rapidly and their ability to proliferate via copious clonal stem production in canopy gaps explains much of their increase in this and possibly other tropical forests.

KEY WORDS

Barro Colorado Island, disturbance ecology, global change, liana increases, Panama, tropical forests

INTRODUCTION

Determining the factors that explain the abundance and distribution of organisms is a central goal in ecology. By ascertaining these factors, ecologists can then formulate process-based explanations for the changes in the

abundance and distribution of those organisms, as well as devise predictions for future shifts with global climate change. One of the major contemporary changes occurring in Neotropical forests is the increase in the density and biomass of lianas (woody vines), often at the expense of trees. Lianas are a common plant growth-form

comprised of thousands of species and with a global distribution similar to that of trees (Schnitzer & Bongers, 2002). In contrast to direct causes of tropical forest change, such as logging or land clearing, increases in liana density and biomass extend to old-growth forests in the absence of direct human activity and are frequently ascribed to global climate change (Schnitzer, 2015; Schnitzer & Bongers, 2011). Liana increases were first documented by Phillips et al. (2002), who surveyed lianas in dozens of forest plots in Central and South America and found that liana density and basal area (BA) were increasing over time. Since then, more than a dozen empirical studies have supported the pattern of increasing liana abundance in Neotropical forests, both in absolute numbers and also relative to trees (e.g. Enquist & Enquist, 2011; Laurance et al., 2014; Yorke et al., 2013). Currently, however, the factors responsible for increasing liana abundance are poorly understood, and no previous study documenting liana increases was able to link these changes to any factor or process (e.g. Marvin et al., 2015; Schnitzer et al., 2020a).

Liana abundance and distribution within tropical forests appear to be largely explained by canopy disturbance (reviewed by Schnitzer, 2018); thus, disturbance has emerged as one of the leading hypotheses to explain increasing liana abundance (Schnitzer & Bongers, 2011). Liana density and BA increase rapidly after both large- and small-scale forest disturbance, presumably because lianas capitalise on high resource availability following disturbance (reviewed by Schnitzer, 2018). For example, lianas recruit aggressively after large, forest-clearing disturbances, such as hurricanes (Hogan et al., 2017; Schnitzer & Bongers, 2002; Webb, 1958), and liana density can exceed that of nearby old-growth forests just 5 years following land abandonment after cattle ranching or farming (Barry et al., 2015). Lianas also respond rapidly to the formation of canopy gaps that occur following the death of a canopy tree, a common form of disturbance in old-growth forests. Many studies have shown that liana density and diversity are far higher in canopy gaps than in the shaded understorey compared to trees (e.g. Dalling et al., 2012; Putz, 1984; Schnitzer & Carson, 2001), and that gaps have been hypothesised to provide an essential regeneration niche for lianas in old-growth forests (Ledo & Schnitzer, 2014). Lianas may proliferate in gaps because of their ability to recruit rapidly via clonal stem production in high-light areas (Peñalosa, 1984; Putz, 1984; Rocha et al., 2020). Lianas also disperse a high proportion of seeds into gaps than into the forest understorey compared to trees (Augspurger & Franson, 1988; Puerta-Piñero et al., 2013); thus, lianas have multiple efficient pathways to effectively recruit into canopy gaps (Schnitzer et al., 2000).

Disturbance could explain increasing liana abundance in several distinct ways. First, if canopy tree mortality rates are increasing, then the greater number of resulting canopy gaps would provide more regeneration niches for lianas. Indeed, the rates of tree mortality have been increasing for decades in many tropical forests; between

1980 and 2010, tree mortality, and thus canopy gap formation, nearly doubled across hundreds of plots in the Amazon basin (McDowell et al., 2020; Yu et al., 2019). Second, other climate change factors, such as increasing CO₂, temperature, nutrient deposition or drought, may interact with disturbance to explain increasing liana abundance (even in the absence of increased tree mortality rates). Third, lianas themselves may be instrumental in increasing their own abundance by acting as ecological niche constructors (*sensu* Olding-Smee et al., 2013), arresting tree regeneration in gaps and modifying environmental conditions to those that favour their own proliferation (Griscom & Ashton, 2003; Schnitzer et al., 2000). If liana abundance exceeds a critical threshold (Marshall et al., 2020), regardless of the cause, then lianas themselves may be able to arrest gap-phase regeneration, resulting in persistent, low-canopy, high-light, liana-dense forest patches that facilitate liana proliferation.

We examined whether liana density and basal area were increasing over a 10-year period (2007–2017) in the Barro Colorado Island, Panama (BCI) 50-ha plot. Previous evidence from BCI suggests that lianas have increased in productivity (Wright et al., 2004), the proportion of trees that they occupy (Ingwell et al., 2010) and in seedling number (relative to trees; Umaña et al., 2020); however, no study has quantified the change in liana sapling and adult abundance in an old-growth forest using a single longitudinal study, nor has any study successfully linked the increase in lianas to disturbance or any other factor (Schnitzer et al., 2020a).

We tested the hypothesis that natural local canopy disturbances are the foci for liana increases (H_1), which we contrasted with the hypothesis that liana increases are independent of canopy disturbance (H_0). We divided hypothesis H_1 into two non-mutually exclusive sub-hypotheses. $H_{1,1}$: recent canopy disturbances provide a regeneration niche for lianas; if so, we should find that increases in liana density and BA are concentrated in recently disturbed canopy gaps. $H_{1,2}$: lianas are niche constructors that actively maintain canopy gaps in a low-canopy state that favour their own proliferation; if so, we should find that increases in liana density and BA are concentrated in gaps that have remained arrested at low-canopy height throughout the study period. Liana increases may also be caused by additive or multiplicative interactions between disturbance and other factors; we provide *a priori* predictions and interpretations for these various possibilities in Table S1.

To test these hypotheses, we used an unparalleled data set of 117,100 liana stems (≥ 1 cm diameter) rooted in the BCI 50-ha plot, which we collected over a 10-year period. In 2007, we conducted the first liana census of the BCI 50-ha plot by measuring the diameter, identifying to species and spatially mapping all rooted liana stems (≥ 1 cm diameter) (Schnitzer et al., 2008, 2012). In 2016–2017, we conducted the second liana census of the BCI plot to test whether liana density and BA increased

over this 10-year period and were concentrated in disturbed forest patches.

MATERIALS AND METHODS

The BCI 50-ha forest dynamics plot is located in an old-growth seasonal tropical moist forest on the central plateau of the island and is arranged as a 1×0.5 km rectangle that is divided into 1250 20×20 m quadrats (Hubbell & Foster, 1983). The BCI plot has not been logged, burned or otherwise manipulated by humans for at least 500 years (Hubbell & Foster, 1983). Descriptions of the geology, climate, flora, fauna and history of BCI can be found in Croat (1978) and Leigh (1999). Descriptions of the BCI plot tree censuses and data set can be found in Condit et al. (2019).

The second liana census of the BCI 50-ha plot

From February 2016 until April 2017, we remeasured the diameter and calculated the growth and mortality of every rooted liana stem from the 2007 census. We quantified liana recruitment by tagging, mapping, measuring the diameter 1.3 m from the last rooting point and identifying to species all newly rooted liana stems ≥ 1 cm diameter that were not present in the previous census. From April to December 2017, we revisited all 1250 quadrats to identify newly recruited stems to the species level, to verify that new liana stems had been mapped correctly and to check whether the new stems were distinct individual lianas or clonal stems. Consistent with the 2007 census, we classified clones as those stems (≥ 1 cm in diameter) that were attached aboveground to another stem in the study but also had their own, independent root system. We followed liana-specific census methods recommended by Gerwing et al. (2006) and Schnitzer et al. (2008, 2012).

We identified liana stems to species in the field using a combination of stem, leaf and flower characteristics. We were able to identify to species 99.4% of the liana individuals; only 328 lianas were left unidentified in 2017, down from 783 in 2007. Of the 328 lianas not identified to species, we were able to classify 24 individuals to the genus *Smilax* (Smilacaceae), one to the genus *Mascagnia spp.* (Malpighiaceae) and one to the genus *Passiflora spp.* (Passifloriaceae).

Quantifying forest disturbance

We determined canopy disturbance throughout the 50-ha plot using two independent data sets that quantified the change in canopy height and canopy tree basal area. We collected canopy height data using high-resolution aircraft and drone-borne LiDAR (light detecting and ranging) in 2009 and 2019 respectively (Appendix S1). With these data, we calculated the geometric mean canopy height per 20×20 m quadrat and ranked each of the 1250

quadrats from lowest to highest canopy height (i.e. high to low disturbance). We then used the changes in canopy height rank to classify the quadrats into four distinct categories. (1) Undisturbed high-canopy forest; the quadrats in the top 20% canopy height rank in both 2009 and 2019 ($n = 185$; Figure S1a). (2) Persistent low-canopy gaps; the quadrats that remained in the lowest 20% canopy height rank in both 2009 and 2019 ($n = 151$; Figure S1b). (3) Recent canopy gaps; the 250 quadrats that lost the greatest canopy height rank from 2009 to 2019 (Figure S1c). (4) Former canopy gaps (recovering forest); the 250 quadrats with the greatest canopy height rank increase from 2009 to 2019 (Figure S1d). We selected these particular four canopy disturbance categories because they allowed us to explicitly test our hypotheses. We excluded 414 quadrats that did not conform to any of the four categories.

We also estimated forest canopy disturbance using the change in canopy tree BA rank per quadrat. We used algorithms from Bohlman and Pacala (2012) parameterised with BA-to-height allometries from Martínez-Cano et al. (2019) to calculate canopy height for all of the trees in the 50-ha plot. We then calculated the geometric mean of the highest canopy layer per quadrat for the 2005 and 2015 censuses and used these data to classify the quadrats into the four disturbance categories described above. Tree BA data were collected in 2005 and 2015; thus, our two disturbance estimates for 2005–2015 and 2009–2019 neatly bracketed our liana surveys from 2007 to 2017.

Data analyses

We tested whether lianas increased on the BCI 50-ha plot by comparing liana density and BA across the entire area from 2007 to 2017. We calculated liana recruitment, mortality and growth of existing stems from 2007 to 2017 across the plot for all rooted stems (both individual and clonal stems) and also separately for clonal stems only.

Prior to testing whether disturbance explained increasing lianas, we found significant positive spatial autocorrelation among quadrats in each canopy disturbance category using Moran's I tests. To remove this autocorrelation, we used a hierarchical clustering algorithm (HDBSCAN) to identify and combine spatially correlated quadrats into individual clusters (Campello et al., 2013). HDBSCAN uses Euclidean distances between quadrats to create a cladogram from which spatially correlated quadrats can be identified (see Appendix S2; McInnes et al. 2007). We selected a minimum cluster size of two quadrats, which is sensitive to autocorrelation at fine spatial scales, thus providing a conservative estimate of autocorrelation while preserving as much data as possible. Final sample sizes were 51, 35, 79 and 65 for the undisturbed forest, persistent low-canopy gaps, recent gaps and former gaps respectively. We confirmed that the final data set included only spatially independent replicates by using Moran's I tests for 4999 permutations in which we

randomly selected one quadrat location per cluster (combined with the non-clustered quadrats) (Figure S9).

We bootstrapped these spatially independent replicates 4999 times (using the mean value for each group of clustered quadrats) and compared the median model estimates of liana recruitment, mortality, growth and the change in liana density and BA among the four canopy disturbance categories using one-way ANOVAs. We used quantile–quantile plots to confirm that the ANOVA residuals were normally distributed. For significant ANOVA results, we used a post hoc test to determine which of the three canopy disturbance categories differed significantly from the undisturbed forest category. Specifically, we subtracted the mean estimate of the undisturbed canopy category from that of each of the disturbed canopy categories and examined whether the 95% confidence intervals around the mean estimate differences overlapped with zero. We examined all stems combined as well as the separate contribution of clonal stems for these analyses.

We repeated this same process using tree BA as a proxy for disturbance. Our results were similar for both estimates of disturbance (LiDAR and tree BA), and thus we present the tree BA data in the supplementary materials (Figures S2, S3; Tables S2, S3). Data were analysed with Python 3 using the Pandas, Numpy and statsmodels packages (Van Rossum & Drake 2018, McKinney, 2010; Harris et al., 2020; Seabold & Perktold, 2010).

RESULTS

Liana density, basal area and species richness in the BCI 50-ha plot

We found a total of 86,723 living rooted liana stems ≥ 1 cm diameter (1734.5 lianas ha^{-1}) in the second census of the BCI 50-ha plot (Figure 1). There were 51,655 small lianas (diameter ≥ 1 cm < 2 cm), 29,583 medium-sized lianas (diameter ≥ 2 cm < 5 cm), 4957 large lianas (diameter ≥ 5 cm < 10 cm)

and 528 extra-large lianas (diameter ≥ 10 cm) (Table 1). These quantities include 34,032 rooted clonal stems (diameter ≥ 1 cm), which contributed 39.2% to total liana stem density (Table 1). The sum of liana BA in the BCI plot was 55.15 m^2 ($1.14 \text{ m}^2 \text{ ha}^{-1}$). Lianas larger than 5 cm diameter contributed nearly half (45.5%) of the total BA while contributing only 6.3% of the total rooted stem density (Table 1). Clonal stem BA across the 50-ha plot was 18.54 m^2 ($0.41 \text{ m}^2 \text{ ha}^{-1}$), accounting for 33.8% of the total liana BA.

In 2017, we identified 175 liana species from 98 genera within 41 families. Thirteen liana species were new to the census in 2017. Liana species were largely concentrated in six plant families: Sapindaceae (22 species), Bignoniaceae (21), Fabaceae (19), Malpighiaceae (16), and Apocynaceae and Dilleniaceae each with nine species. Six families had five to eight liana species and 29 families had four or fewer liana species. The 10 most abundant liana species comprised 46.5% of the rooted liana stems and 36.7% of the liana BA (Table 2). Ninety liana species had at least 100 separately rooted stems, 22 species had 50 to 100 separately rooted stems, 38 species had three to 50 stems and 25 species had only one or two separately rooted stems in the entire 50-ha plot.

The mean percentage of clonal stems for the 10 most common species was high (41%), with substantial variation among species. For example, 56.9% of the 12,498 rooted stems of *Coccoloba excelsa*, the most abundant species in the BCI plot in both 2007 and 2017, were clonal (Table 2). Clonal stem percentages for *Maripa panamensis* and *Petrea volubilis*, two of the 10 most common species with the lowest percentage of clonal stems, were 17.6% and 16.4% respectively (Table 2).

Increasing liana density and basal area in the BCI 50-ha plot

From 2007 to 2017, liana density across the 50-ha plot increased 29.2% (19,578 stems), from 67,145 to 86,723. Liana

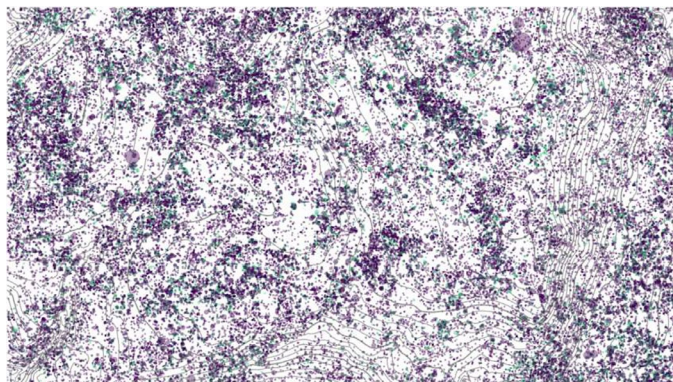


FIGURE 1 Map of the rooted liana stems ≥ 1 cm diameter on the Barro Colorado Island, Panama 50-ha plot. The plot is 1 km on the x-axis and 0.5 km on the y-axis. The purple points represent the principal liana stems; green points represent clonal stems that are still attached to the principal stem but have their own root system. The relative diameter of each stem is indicated by the relative size of the point. The grey lines represent elevational contours of the plot

TABLE 1 Static, dynamic and demographic data from the second census of the lianas of the Barro Colorado Island, Panama 50-ha plot

	Entire 50-ha plot 2017				Change from 2007 to 2017				Demography 2007–2017			
	Density	Basal area (m ²)	Richness	Density change	Basal area change (m ²)	Recruitment	Mortality	Persistent stems	Persistent stem transition	Persistent stem ingrowth	Persistent stem outgrowth	
Total stems												
Small (1–1.9 cm)	51,655	7.75	164	16,377	1.70	36,180	15,964	13,453	–3839	2022	5861	
Medium (2–4.9 cm)	29,583	22.15	159	2787	2.16	12,502	12,041	11,253	2326	5828	3502	
Large (5–9.9 cm)	4957	17.21	122	382	1.54	1191	2150	1968	1341	1798	457	
Extra-large (≥10 cm)	528	8.02	69	32	0.73	81	222	233	173	214	41	
Total	86,723	55.13		19,578	6.13	49,954	30,377	26,907	1	9862	9861	
Clonal stems												
Small (1–1.9 cm)	20,751	3.02	143	9084	1.19	16,406	5972	3898	–1350	447	1797	
Medium (2–4.9 cm)	11,412	8.08	131	3952	2.74	6864	3798	2771	886	1777	891	
Large (5–9.9 cm)	1735	5.72	88	696	2.38	771	497	453	422	511	89	
Extra-large (≥10 cm)	134	1.72	36	65	0.8	53	31	31	43	50	7	
Total	34,032	18.54		13,797	7.11	24,094	10,298	7153	1	2785	2784	

Static data include liana density, basal area and species richness in 2017. Dynamic data include the change in liana density and basal area from 2007 to 2017. Demographic data include liana recruitment, mortality and persistence from 2007 to 2017. Persistent stem transition is the net persistent stems that transitioned from one size class to another, separated into the number of persistent stems that recruited into (ingrowth) and out of (outgrowth) each size class. Persistent stem ingrowth into the small size class was the result of the loss of stem diameter from the first census. Stem data are divided into small, medium, large, extra-large and total stems for all rooted stems (top) and for all rooted clonal stems (bottom). [Correction added on 1 October 2021, after first online publication: The values under the Richness column of Table 1 have been corrected in this version.]

TABLE 2 Ten most abundant liana species in the Barro Colorado Island, Panama 50-ha plot in 2017

Species	Family	Total stem density	% Clonal stem density	Total basal area (m ² 50 ha ⁻¹)	% Clonal basal area	Total stem recruitment	Total stem mortality	% stem increase
<i>Coccoloba excelsa</i>	Polygonaceae	12,498	56.9	3.47	44.1	7699	3134	57.5
<i>Hiraea reclinata</i>	Malpighiaceae	4368	28.1	1.79	21.5	2080	1184	25.8
<i>Paragonia pyramidata</i>	Bignoniaceae	3718	43.8	2.38	34.0	1989	1823	4.7
<i>Dolioscarpus olivaceus</i>	Dilleniaceae	3639	45.7	1.12	31.7	1495	780	24.5
<i>Maripa Panamensis</i>	Convolvulaceae	3414	17.6	2.83	11.3	1724	1261	15.7
<i>Prionostemma asperum</i>	Celastraceae	3337	57.0	4.58	38.3	1165	1032	4.2
<i>Petrea volubilis</i>	Verbenaceae	3066	16.4	1.00	14.5	1191	737	17.4
<i>Dolioscarpus major</i>	Dilleniaceae	2662	31.2	1.08	20.3	1286	682	29.3
<i>Mascagnia hiraia</i>	Malpighiaceae	1816	21.8	0.96	18.9	990	569	30.2
<i>Aegiphila cephalophora</i>	Verbenaceae	1766	38.0	1.23	32.0	1293	982	21.4

Data are presented for the total rooted stem density, percentage of clonal stems, total basal area, percentage of basal area contributed by clonal stems, total stem recruitment and mortality from 2007 to 2017 and the per cent stem increase from 2007 to 2017.

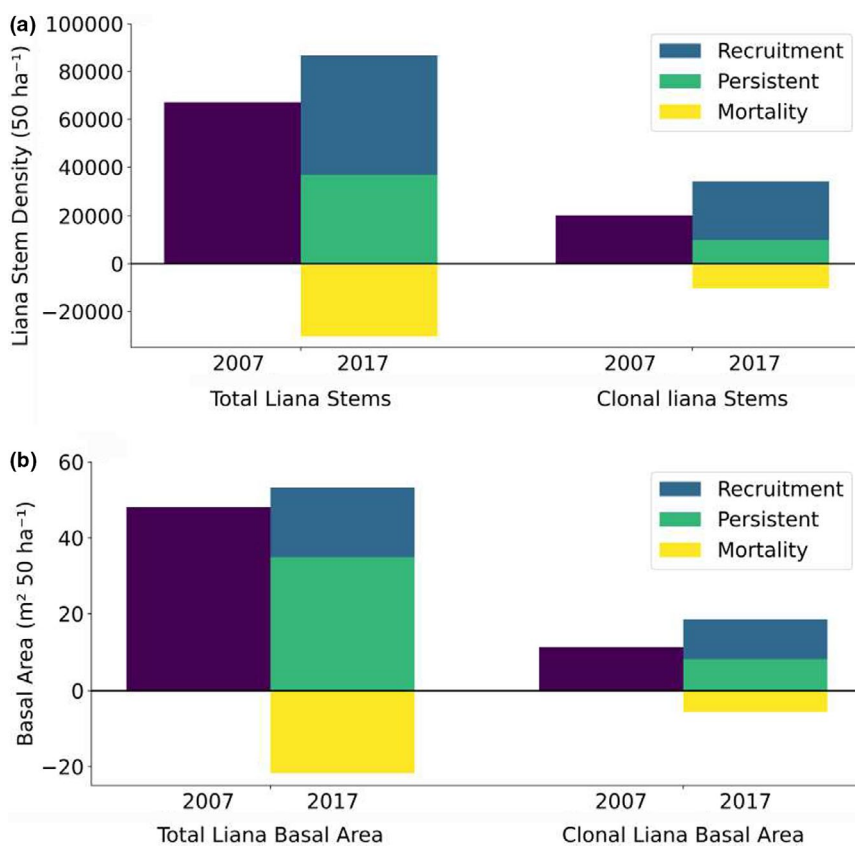


FIGURE 2 The change in liana density (a) and basal area (b) from 2007 (monochromatic purple bar) to 2017 (multichromatic bar) for all rooted stems ≥ 1 cm diameter on the Barro Colorado Island, Panama 50-ha plot. Liana density (a) increased by 29.2% during this 10-year period, primarily due to the higher stem recruitment (blue) and persistence (green) compared to mortality (yellow) for all rooted stems combined and for rooted clonal stems (≥ 1 cm diameter). Liana basal area (b) increased 12.5% due to the combination of higher stem recruitment (blue) and growth of persistent stems (green) compared to mortality (yellow) for all rooted stems combined and for rooted clonal stems separately. These analyses included all liana stems ≥ 1 cm diameter across the entire 50-ha area

density increased due to massive new stem recruitment (49,955), which was balanced only partially by the mortality of 30,377 stems (Table 1; Figure 2a). Stem density

increased for 118 liana species, decreased for 39 species and remained the same for five species. Each of the 10 most common liana species increased in stem density;

however, the degree of increase varied considerably, from 4.2% for *Prionostemma asperum* to a stunning 57.5% for *Coccoloba excelsa* (Table 2).

Clonal stem production explained most of the liana density increase. Clonal stem density was 68.2% higher in 2017 than that in 2007 (34,032 vs. 20,235; Figure 2a). Liana clonal stem recruitment contributed nearly half (48.2%) of total stem recruitment (24,095 vs. 49,995); however, clonal stem mortality was only one third (33.9%) of total stem mortality (10,298 vs. 30,377). Therefore, clonal stem accumulation (recruitment minus mortality) contributed 70.5% (13,796) of the 19,577 new rooted stems in the 2017 census.

Liana BA increased by 12.5% (6.14 m²), from 49.01 m² to 55.15 m² from a combination of growth of existing stems (8.90 m²) plus recruitment of new stems (19.45 m²) minus stem mortality (22.22 m²; Figure 2b). Clonal stem

BA was 62.1% higher in 2017 than that in 2007 (18.54 m² vs. 11.44 m²; Figure 2b), contributing considerably to the increase in total liana BA. The net gain of 7.11 m² of clonal stem BA was due to the growth of existing clonal stems (2.47 m²) plus recruitment (10.28 m²) minus mortality (5.64 m²). Non-clonal stem BA actually decreased by 0.97 m² during this period.

Disturbance and increasing liana density and basal area

Liana density and BA in 2017 were more than two times higher in the persistent low-canopy gaps and ~50% higher in the recently disturbed and formerly disturbed gaps than in the undisturbed high-canopy forest (Figure 3).

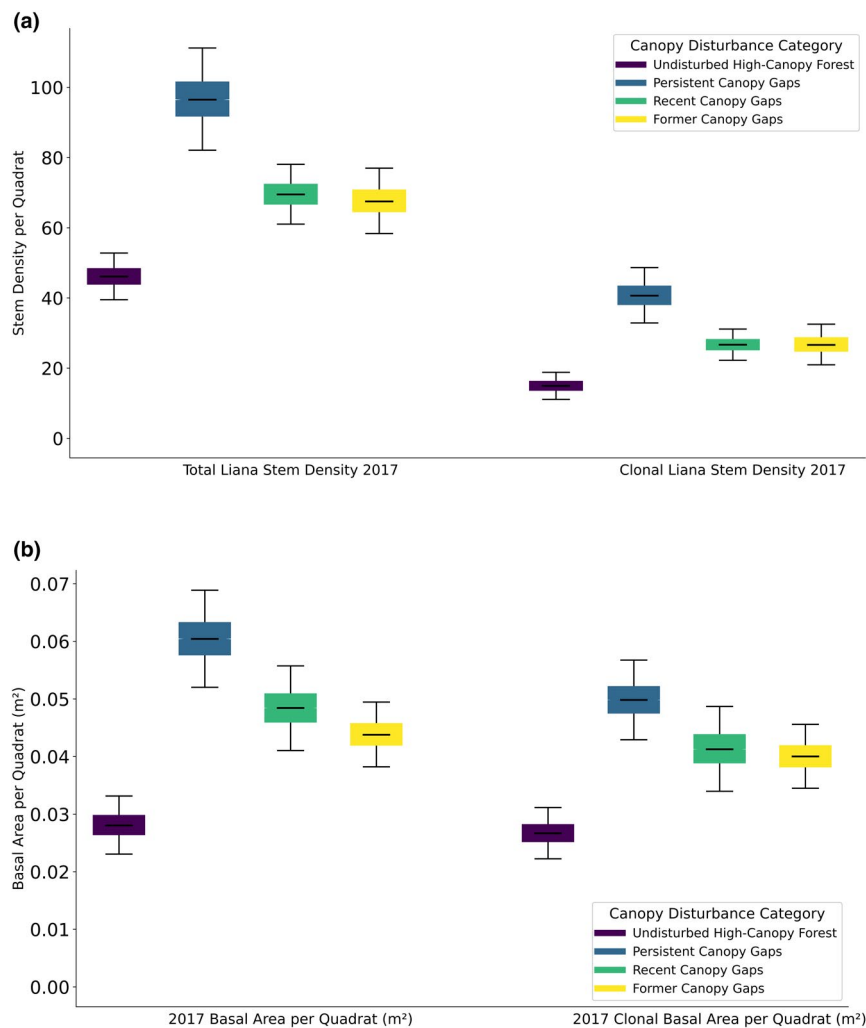


FIGURE 3 Modelled estimates of mean per-quadrat 2017 stem density (a) and basal area (b) of lianas ≥ 1 cm diameter on the Barro Colorado Island, Panama 50-ha plot for four canopy disturbance categories—undisturbed high-canopy forest, persistent low-canopy gaps, recent canopy gaps and former canopy gaps (Figure S1). For each canopy disturbance category, quadrat heights were tested for autocorrelation; correlated sites were clustered and represented by a single mean value. Clustered and non-clustered (single) quadrats for each canopy disturbance category were bootstrapped and compared 4999 times to calculate differences in the means and variance for all rooted stems combined and for rooted clonal stems separately. The horizontal line within each coloured bar represents the estimated mean, the notch, where visible, represents the 95% confidence interval of the mean, the coloured bar represents the 25% and 75% quartiles of the data and the whiskers represent the 5% and 95% range of the data. Canopy heights were measured with LiDAR in 2009 and 2019 (Appendix S1)

Clonal stem density and BA reflected the same patterns as the total stem data (Figure 3).

The increase in liana density was the highest in the persistent low-canopy gaps followed by the recent gaps and former gaps, and lowest in the undisturbed forest (Figure 4a; Table S4). The increase in liana density was the result of high stem recruitment minus lower stem mortality in each of the canopy disturbance categories (Figure 4a). The increase in clonal liana density was particularly prominent in the persistent low-canopy gaps, driven largely by a high clonal stem recruitment (Figure 4b).

Liana BA increased the most in the persistent low-canopy gaps, followed by the recent gaps and former gaps, and lowest in the undisturbed high-canopy forest (Figure 4c; Table S5). The gain in BA from liana recruitment was balanced by the loss from stem mortality for all canopy disturbance categories; thus, net liana BA gain was due mostly to the growth of existing stems (Figure 4c). Clonal stem recruitment contributed substantially to liana BA increase, particularly for the persistent low-canopy gaps, where clonal recruitment

substantially outpaced the loss from mortality or the gain from growth of existing stems (Figure 4d; Table S5). We found similar results using tree BA as our estimate of disturbance (Figures S3 and S4–S7; Tables S2, S3).

DISCUSSION

Our data strongly support the hypothesis that canopy disturbances are foci for increasing liana abundance on BCI; 86% of the increase in liana density and BA were in the three canopy gap categories compared with only 14% in the undisturbed, high-canopy areas. Liana increases were prevalent in recent canopy gaps and, to a lesser degree, in recovering (former) canopy gaps compared to the high-canopy forest patches. However, the major increases in liana density and BA were in persistent low-canopy gaps. Nearly half of all liana recruitment (48.5%) and new stem BA (52%) were in the persistent low-canopy gaps, a finding that is consistent with the hypothesis that lianas are ecological niche constructors.

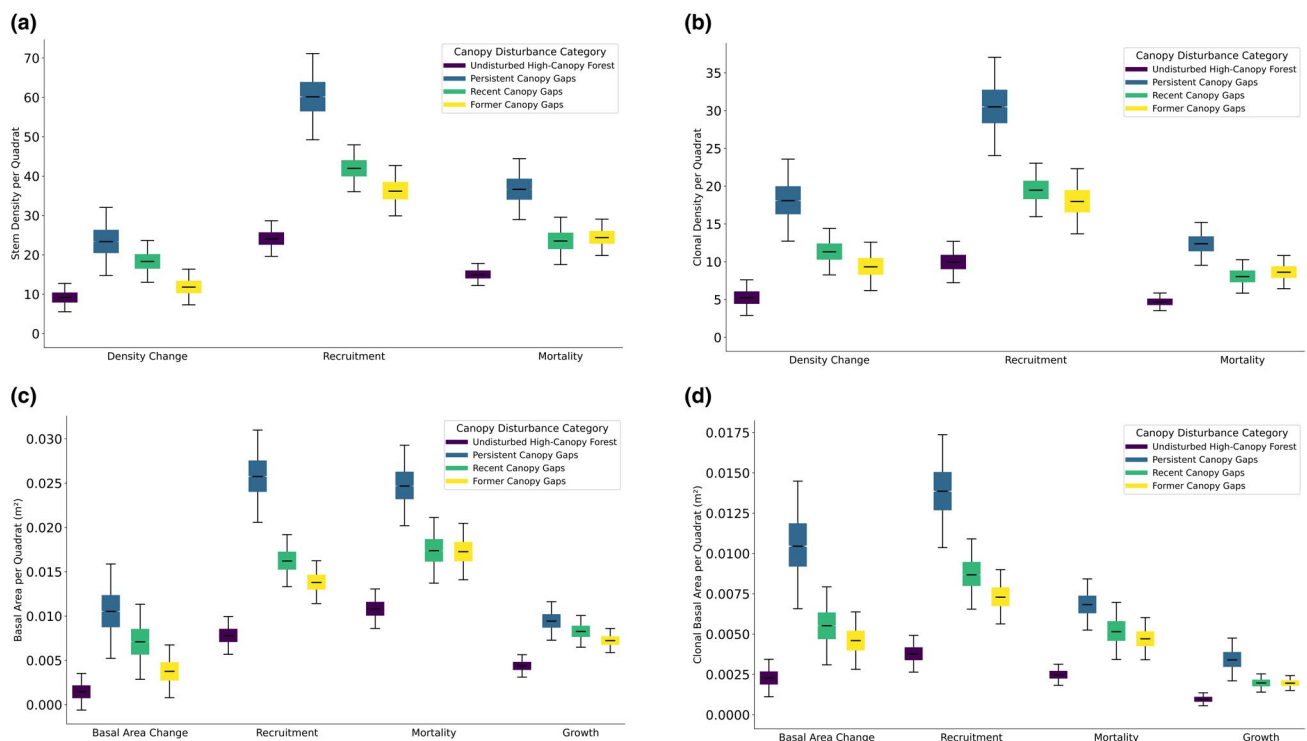


FIGURE 4 Modelled estimates of mean change in (a) liana stem density; (b) clonal stem density; (c) liana stem basal area; and (d) clonal stem basal area from 2007 to 2017 on the Barro Colorado Island, Panama 50-ha plot. The four canopy disturbance categories were as follows: undisturbed high-canopy forest, persistent low-canopy gaps, recent canopy gaps and former canopy gaps (Figure S1). For each canopy disturbance category, quadrats were tested for autocorrelation in disturbance (canopy height); correlated sites were clustered and represented by a single mean value. Clustered and non-clustered (single) quadrats for each canopy disturbance category were bootstrapped and compared 4999 times to calculate differences in the means and variance for all rooted stems combined and for rooted clonal stems separately. Liana stem density change (panels a and b) is divided into recruitment and mortality. Liana basal area change (panels c and d) is divided into recruitment, mortality and growth. Density and basal area data are based on all rooted liana stems (≥ 1 cm diameter) in each canopy disturbance category. For each canopy disturbance category, the horizontal line represents the estimated mean, the notch, where visible, represents the 95% confidence interval of the mean, the coloured bar represents the 25% and 75% quartiles of the data and the whiskers represent the 5% and 95% range of the data. Canopy heights were measured with LiDAR in 2009 and 2019 (Appendix S1)

Disturbance as a nuanced explanation for increasing liana abundance

The pattern of increasing tree mortality, and thus canopy gap formation, is occurring in tropical forests worldwide (McDowell et al., 2018, 2020), which likely contributes to increasing liana abundance in many tropical forests. On the BCI 50-ha plot, however, canopy tree mortality has been highly variable over the past 30 years (Rutishauser et al., 2020) but has increased only slightly since 1990 (Condit et al., 2017). Therefore, highly elevated rates of canopy gap creation are an unlikely explanation for the liana increases in the BCI forest.

There are several hypotheses to explain how canopy gaps are contributing to increasing liana abundance on BCI. First, exogenous climate change factors, such as elevated temperature, CO₂, drought and nutrient deposition, all of which have been hypothesised to favour tropical lianas over trees (Schnitzer et al., 2011, 2020a), may be conspiring with disturbance to provide an environment amenable to liana increases. That is, changing exogenous factors may be potentiating the ability of lianas to respond to disturbance. However, the relatively small increase in lianas in undisturbed forest suggests that such exogenous factors alone have a minor effect when not combined with disturbance. We do not know which exogenous factors have previously conspired or are currently conspiring with disturbance to enhance liana proliferation.

Alternatively, by initiating the pattern of increasing liana abundance, exogenous factors may have pushed liana density past a critical threshold that subsequently allowed lianas to more effectively proliferate in gaps (Marshall et al., 2020). That is, endogenous factors (e.g. liana critical mass) may have eclipsed the contribution of the exogenous factors that were the initial catalyst for increasing liana abundance. When lianas reach high abundance in canopy gaps they can dominate for decades, extending the time that gap regeneration remains arrested and thus maintaining the very conditions that favour their own proliferation (Baleé & Campbell, 1990; Schnitzer et al., 2000; Tymen et al., 2016). If liana proliferation in persistent low-canopy gaps can enlarge the size of gaps over time, they may provide a net increase in high-light areas that favour additional liana recruitment and result in increased liana accumulation, thus explaining the increase in liana abundance in this forest. Indeed, persistent low-canopy, liana-dominated areas appear to be expanding in size on BCI since 1985, and many small low-canopy areas have coalesced and enlarged over the past 35 years (M. Visser unpublished). The expansion of persistent low-canopy gaps is not unique to BCI; a similar phenomenon was observed in the Bolivian Amazon, where the size of liana-dense, low-canopy gaps increased 59% from 1986 to 2000 (Foster et al., 2008).

Lianas as ecological niche constructors

Much of the increase in liana abundance on BCI appears to be caused by the proliferation of lianas in persistent low-canopy gaps, supporting the hypothesis that lianas are ecological niche constructors. Lianas likely begin the niche constructor process by killing canopy trees, which has been reported in several studies (e.g. van der Heijden et al., 2015; Ingwell et al., 2010). By killing canopy trees, lianas create canopy gaps (disturbances), essentially constructing the very environment that favours their own regeneration (Putz, 1984). Creating disturbances, however, is only the first step in the niche construction process. The second, and perhaps more important step, is that lianas actively maintain gaps in a low-canopy state by clogging gaps with stem and leaf proliferation, thereby arresting tree regeneration and preventing the gap from regaining a high canopy (Schnitzer et al., 2000). As lianas continue to recruit and grow in the persistent low-canopy gap, they further clog and expand the gap, creating a positive feedback of liana recruitment. Indeed, when lianas were experimentally removed from gaps, tree recruitment, growth and diversity increased, and those gaps began to regenerate a tall canopy (Schnitzer & Carson, 2010; Schnitzer et al., 2014). In other words, once lianas are removed, the conditions that allow them to proliferate begin to disappear and canopy gaps return to a high-canopy state.

The unique capacity of lianas to survive treefalls and then to produce copious clonal stems in post-disturbance canopy gaps may explain their ability to act as ecological niche constructors (Peñalosa, 1984; Putz, 1984; Rocha et al., 2020). Clonal stem recruitment contributed disproportionately to increasing liana stem density and BA, especially in the persistent low-canopy gaps. From 2007 to 2017, the increase in liana density and BA was higher for clonal stems than for non-clonal stems for all but the smallest stem size class (Table 1). Thus, clonal stem recruitment and growth in persistent low-canopy gaps were largely responsible for increasing liana abundance in the BCI forest.

Ramifications of increasing liana abundance

The dramatic increase in lianas that we observed can substantially alter the functioning of tropical forests. Lianas substantially depress tree performance (da Cunha Vargas et al., 2020; Schnitzer & Bongers, 2002; Toledo-Aceves, 2015); experimental evidence has shown that lianas significantly reduce tropical tree growth, recruitment, reproduction and survival (Estrada-Villegas & Schnitzer, 2018; Garcia-Leon et al., 2018). As lianas increase in abundance, so may their negative effects on such emergent processes as forest-level carbon sequestration and storage (van der Heijden et al., 2013; Schnitzer et al., 2014), as well as tree diversity and

composition (Schnitzer, 2018). Tropical forests store more than 40% of all terrestrial carbon (Phillips et al., 2009), and because much of that carbon is in the trunks of large trees, the negative effects of lianas on tree growth and survival suppresses the ability of tropical forests to sequester and store carbon (van der Heijden et al., 2013; Ledo et al., 2016). Lianas may also influence tree species diversity, relative abundance and community composition by negatively affecting some tree species more than others (e.g. Carsten et al., 2002; Putz, 1984; Visser et al., 2018). However, not all effects of lianas are negative; lianas positively influence many animal species, which depend on lianas for food and forest structure (Adams et al., 2019; Arroyo-Rodríguez et al., 2015; Odell et al., 2019; Schnitzer et al., 2020b). Increasing liana density and biomass could alter the relative abundance and diversity of animal species, as well as their trophic interactions—a hypothesis that remains untested. Finally, liana dynamics and turnover may be faster than those of other tropical forest elements, such as trees (Ingwell et al., 2010; Phillips et al., 2005); thus, changes in liana abundance may be a harbinger of additional impending effects of climate change on tropical forests.

The increase in liana density and BA over the past decade on the BCI plot is unsustainable if tropical forests are to remain in their current physiognomic state. If liana density was to continue to increase annually by 2.9%, the number of lianas rooted in the BCI plot in 2007 (67,145) would double by the year 2032, triple by 2046 and quadruple to 268,580 rooted stems (5450 ha^{-1}) by 2056. Accurately predicting future liana densities, however, remains a challenge because the factors that regulate liana density, diversity, biomass and productivity in tropical forests remain poorly understood (di Porcia e Brugnara et al., 2019; Schnitzer et al., 2016; Muller-Landau & Pacala, 2020; Verbeeck & Kearsley, 2016).

Long-term liana increases on Barro Colorado Island and other tropical forests

The 2.9% annual increase in liana density and BA on the BCI 50-ha plot is consistent with previous reports from other forests. For example, in a nearby old-growth forest on Gigante Peninsula, liana density increased 1.6% per year from 2013 to 2018 (Schnitzer et al., 2020a). In Central Amazonia, from 1999 until 2012, liana density increased 1% annually in thirty-six 1 ha^{-1} plots arrayed over 600 km^2 of old-growth forest (Laurance et al., 2014). Phillips et al. (2002) reported that from 1981 until 2001, lianas >10 cm diameter had increased more than 4% annually in Amazonian forests. Thus, the striking increase in liana abundance on BCI does not appear to be a unique phenomenon.

The liana increase that we found on BCI over the past decade may reflect much longer term dynamics

that have been in motion for more than 50 years—since at least the 1960s. Evidence for this claim comes from historical data on the percentage of large trees carrying lianas, based on surveys from 1968 to 1969, 1980, 1996 and 2007 (Schnitzer et al., 2012; Wright et al., 2004). For example, the percentage of trees (>20 cm diameter) that hosted lianas on the central plateau on BCI increased 57% from 43 to 47% in 1980 (Putz, 1984) to 73.6% in 2007 (Ingwell et al., 2010). This annual increase of more than 2% is consistent with our findings. Knight (1975) reported that in 1968–69, 32% of the trees >10 cm diameter on BCI had lianas in their crowns compared to 53% of the >10 cm diameter trees in 2007 (Ingwell et al., 2010). This 65% difference over the 39-year period is a 1.7% annual increase in the percentage of trees that hosted lianas. If liana infestation is a reliable estimate for the change in liana density (Wright et al., 2015), then the striking increase in lianas that we found has been occurring for far longer than previously recognised on BCI and perhaps in many other tropical forests.

As liana abundance continues to increase over time, their ability to suppress gap-phase regeneration may also increase, resulting in a growing accumulation of persistent low-canopy, liana-suppressed gaps. If so, the rate of liana increase may also accelerate since liana recruitment is highest in these low-canopy, liana-dense gaps. Tropical forests may continue to accumulate lianas until they reach a new stable equilibrium, where liana recruitment is once again balanced by liana mortality. Alternatively, lianas could continue to increase in abundance on BCI, eventually changing much of the high-canopy forest to low-canopy liana-dominated forest, a forest type that covers vast areas across the tropics (e.g. Pérez-Salicrup et al., 2001; Pires & Prance, 1985; Tymen et al., 2016; Webb, 1958).

CONCLUSIONS

From 2007 until 2017, liana density increased by 29.2% and liana BA by 12.5% in an old-growth forest on Barro Colorado Island. These massive increases may be part of a 50-year trend of increasing lianas in this forest, which has profound ramifications for the future of BCI and similar tropical forests. The impressive increase in lianas was associated primarily with disturbance, supporting the hypothesis that disturbance contributes to increasing liana abundance in Neotropical forests. Liana recruitment predominated in persistent low-canopy, liana-dense gaps, lending support to the hypothesis that lianas are ecological niche constructors, creating and maintaining persistent low-canopy gaps that promote their own recruitment and growth, and thus explaining much of the recent liana increase on BCI. Exogenous factors, such as those associated with climate change, may be interacting with disturbance to

create an environment favourable to accelerated liana proliferation. Our findings, along with evidence from other studies, document a sustained pattern of increasing liana abundance on BCI and in other tropical forests. The ability of lianas to both increase and capitalise on disturbance, and the interaction between disturbance and exogenous factors, may be largely responsible for the phenomenon of increasing lianas in Neotropical forests.

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AUTHORSHIP

S.A. Schnitzer conceived the conceptual idea for the manuscript, wrote the manuscript and led the liana data collection efforts. D.M. DeFilippis helped with the conceptual development, conducted post-field data quality assurance, data management and the statistical analyses, and also commented on the manuscript. M. Visser and S. Estrada-Villegas helped with the conceptual development and commented on the manuscript. R. Rivera-Camaña, B. Bernal, S. Pérez, A. Valdéz, S. Valdéz and A. Aguilar collected field data, managed field data collection and conducted in-field data quality control and species identification. J. Dalling, E. Broadbent, A. Almeyda Zambrano and M. Visser provided LiDAR data and commented on the manuscript. S.P. Hubbell conceived the 50-ha plot concept, contributed to the ideas for the initial liana census and commented on the manuscript. Maria Garcia-Leon coordinated the logistics for the liana census, including managing field and data entry technicians.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data supporting the results of this paper are available in Dryad (<https://datadryad.org/stash/dataset/doi:10.5061/dryad.7sqv9s4sm>). [Correction added on 9 October 2021, after first online publication: The data doi has been added to the Data Availability Statement in this version.]

ORCID

Stefan A. Schnitzer  <https://orcid.org/0000-0002-2715-9455>
 David M. DeFilippis  <https://orcid.org/0000-0003-4040-8003>
 Marco Visser  <https://orcid.org/0000-0003-1200-0852>
 Sergio Estrada-Villegas  <https://orcid.org/0000-0002-1072-4921>
 James W. Dalling  <https://orcid.org/0000-0002-6488-9895>
 Eben N. Broadbent  <https://orcid.org/0000-0002-4488-4237>
 Angelica M. Almeyda Zambrano  <https://orcid.org/0000-0001-5081-9936>
 Stephen P. Hubbell  <https://orcid.org/0000-0003-2797-3411>

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