The response of lianas to 20 yr of nutrient addition in a Panamanian forest

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Abstract. Over the past two decades, liana density and basal area have been increasing in many tropical forests, which has profound consequences for forest diversity and functioning. One hypothesis to explain increasing lianas is elevated nutrient deposition in tropical forests resulting from fossil fuels, agricultural fertilizer, and biomass burning. We tested this hypothesis by surveying all lianas ≥1 cm in diameter ($n = 3,967$) in 32 plots in a fully factorial nitrogen (N), phosphorus (P), and potassium (K) addition experiment in a mature tropical forest in central Panama. We conducted the nutrient-addition experiment from 1998 until present and we first censused lianas in 2013 and then again in 2018. After 20 yr of nutrient addition (1998–2018), liana density, basal area, and rarefied species richness did not differ significantly among any of the nutrient-addition and control treatments. Moreover, nutrient addition in the most recent 5 yr of the experiment did not affect liana relative growth, recruitment, or mortality rates. From 2013 until 2018, liana density, basal area, and species richness increased annually by 1.6%, 1.4%, and 2.4%, respectively. Nutrient addition did not influence these increases. Our findings indicate that nutrient deposition does not explain increasing lianas in this tropical forest. Instead, increases in tree mortality and disturbance, atmospheric carbon dioxide, drought frequency and severity, and hunting pressure may be more likely explanations for the increase in lianas in tropical forests.

Key words: Barro Colorado Nature Monument; Gigante Peninsula; lianas; nitrogen; nutrients; Panama; phosphorus; potassium.

Introduction

Global change is altering all ecosystems on earth, and even ecosystems once thought to be largely buffered from climate change, such as tropical forests, are now changing. One of the most notable changes in neotropical forests is the increase in liana density, productivity, and biomass. There are now more than a dozen studies demonstrating that lianas are increasing in density, biomass, or productivity in mature neotropical and subtropical forests (reviewed by Schnitzer and Bongers 2011, Schnitzer 2015). The increase in liana abundance or biomass, either relative to trees or in absolute terms, has been reported for forests from Argentina, the Bolivian and Brazilian Amazon, Costa Rica, French Guiana, India, Panama, and Puerto Rico, as well as the subtropical southeastern United States (Phillips et al. 2002, Wright et al. 2004, Allen et al. 2007, Schnitzer et al. 2012, Laurance et al. 2014, Pandian and Parthasarathy

2016, Ceballos and Malizia 2017, Hogan et al. 2017, Umaña et al. 2020).

The increase in liana density and biomass is alarming because lianas alter tree diversity and community composition, as well as reduce tree growth and the capacity of tropical forests to uptake and store carbon. Lianas reduce tree growth, survival, reproduction, recruitment, and species diversity (Toledo-Aceves 2015, Garcia-Leon et al. 2018). The severity of the effects of lianas varies with the identity of their tree host species, which can shift the competitive balance among co-occurring tree species and thus influence tree species composition and diversity (Schnitzer 2018, Muller-Landau and Visser 2019). At the ecosystem level, lianas decrease whole-forest carbon sequestration and storage (van der Heijden et al. 2013), reduce available soil moisture during seasonal droughts (Reid et al. 2015), and alter forest nutrient fluxes (Asner and Martin 2015, van der Heijden et al. 2015).

Lianas also influence animal species diversity and community composition. A wide variety of animals, including invertebrates, arboreal mammals, and many bird species use lianas as a food source, eating liana leaves, pollen, flowers, and fruits (Odell et al. 2019). Many invertebrate herbivores specialize on liana species

(Ødegaard 2000), and insectivorous bird species may feed on these specialized herbivores (Schnitzer et al. 2020). Climbing animals such as monkeys, sloths, rodents, and ants depend on the structure and connectivity that lianas provide in the forest canopy (Chiarello et al. 2004, Adams et al. 2019). Therefore, increasing liana abundance may have a substantial effect on both plant and animal diversity and composition, as well as tropical forest functioning.

Despite the potential ramifications of increasing liana abundance in neotropical forests, we know little about the factors responsible for this phenomenon (Schnitzer 2015). One hypothesis for increasing liana abundance is the global increase in nutrient deposition (Schnitzer et al. 2011, Asner and Martin 2015). Fossil fuels, agricultural fertilizers, and biomass burning have dramatically increased nutrient deposition, and both terrestrial and aquatic ecosystems have been fertilized by anthropogenically derived nutrients (Hietz et al. 2011, Kanakidou et al. 2016). For example, soluble nitrogen deposition has increased nearly threefold since 1850 (Kanakidou et al. 2016). Compared to co-occurring trees, lianas have relatively high concentrations of nitrogen, phosphorus, potassium, and calcium in their leaves (Wyka et al. 2013, Asner and Martin 2015). Increasing nutrient fertilization may advantage lianas by allowing them to satisfy their higher resource needs, which could increase their photosynthetic capacity and thus their growth and survival rates (Schnitzer et al. 2011, Asner and Martin 2015). Indeed, plants that have high nutrient demands (and thus are nutrient limited) tend to respond more to nutrient addition than plants with lower nutrient demands (Chapin et al. 1986). In addition, lianas allocate a larger ratio of their resources to leaves rather than to a large supportive trunk (compared to trees), resulting in a relatively high ratio of photosynthetic tissue per whole-plant biomass (Wyka et al. 2013, Isnard and Feild 2015). If nutrient deposition accelerates liana growth, then lianas would add increasingly more leaf mass as they grow, thus furthering their growth advantage over co-occurring trees (Asner and Martin 2015, Isnard and Feild 2015). Thus, greater nutrient demand combined with greater allocation to leaves could combine to explain increases in liana density and biomass relative to trees in tropical forests subjected to anthropogenic nutrient deposition.

Evidence for the effects of nutrients on liana density, diversity, distribution, and performance is mixed. In Sabah, Malaysia liana basal area and species richness were higher in forests with relatively nutrient-rich alluvial soils compared to nutrient-poor sandstone and kerangas (heath) forest; however, liana density did not differ among forests (DeWalt et al. 2006). By contrast, in Panama, soil chemistry had little effect on liana density, richness, or distribution in the Barro Colorado Island 50-ha plot (Dalling et al. 2012, Ledo and Schnitzer 2014) and in 22 secondary dry forest plots (Estrada-Villegas et al. 2020). In the only experimental study comparing the effects of nutrients on lianas and trees, phosphorus addition increased seedling photosynthetic performance for seven liana and six tree species in the shaded understory (in central Panama); however, the relative performance of lianas and trees did not differ (Pasquini et al. 2015).

Whether long-term nutrient deposition influences liana sapling and adult liana performance and abundance and whether it explains the recent increase in lianas in neotropical forests have never been tested experimentally. Here we used a 20-yr nutrient-addition experiment (1998–2018) conducted in a mature tropical forest to test the hypothesis that elevated nutrient deposition explains increasing liana density and basal area in tropical forests. Our rationale was that if nutrient deposition is a strong contributor to the observed increase in liana abundance over recent decades, then we should detect greater liana stem density, basal area, and species richness after 20 yr of nutrient addition compared to control plots. We also examined the dynamic changes in liana density, basal area, species richness, growth, recruitment, and mortality during the most recent 5 yr of the experiment (from 2013 until 2018), anticipating strong responses after 15 yr of nutrient addition because of the lag in whole plant and stand-level responses to nutrient additions. This study is the most comprehensive to date on the demographic response of lianas to nutrient addition in tropical forests, and it is the first experimental test of the liana–nutrient deposition hypothesis.

Materials and Methods

We conducted this study from 1998 until 2018 in a ~600-yr-old (C. McMichael, *personal communication*) seasonally moist, lowland tropical forest located on Gigante Peninsula, a protected mainland forest that is part of the Barro Colorado Nature Monument, Republic of Panama (Turner et al. 2015, Wright et al. 2018). Annual rainfall averages ~2,600 mm, with a dry season from approximately mid-December until late April. Soils are Oxisols and Inceptisols and are relatively infertile compared to other soils in central Panama (Yavitt et al. 2009).

Plot setup and nutrient addition

In 1998, we established 32 40 × 40 m plots in a 38.4-ha area, where we surveyed and mapped trees >20-cm diameter at breast height (DBH). Tree species distributions (S. J. Wright, *unpublished data*) and prior soil surveys (Yavitt et al. 2009) suggested an initial southwest to northeast soil nutrient gradient paralleling a 30-m elevational gradient across the 38.4-ha area. We therefore adopted an incomplete block design with four replicates aligned from north to south and two blocks aligned from east to west within each replicate. We assigned the N, P, K, and NPK vs. the NP, NK, PK, and control

treatments randomly to blocks within each replicate and treatments randomly to plots within blocks. This incomplete block design controls spatial variation at the cost of sacrificing power to evaluate the three-way NPK interaction (Winer 1971). Beginning in 1998, we added nutrients four times each wet season in May, July, September, and October (see Wright et al. 2018). Nutrient additions totaled 125 kg $N \cdot ha^{-1} \cdot yr^{-1}$ (coated urea: $(NH_2)_2CO$), 50 kg $P \cdot ha^{-1} \cdot yr^{-1}$ (triple super phosphate: $Ca(H_2PO_4)_2 \ H_2O$), and 50 kg $K \cdot ha^{-1} \cdot yr^{-1}$ (potassium chloride: KCl). The added N, P, and K were approximately 69%, 470%, and 88%, respectively, of the annual inputs that would be derived from fine litter in a nearby forest and far higher than background nutrient input from the atmosphere (Wright et al. 2018).

Plant surveys

We first surveyed lianas in the 32 plots from April through mid-July 2013, and then again from August to mid-September 2018. We did not survey the lianas prior to the start of the experimental manipulation because the pattern of liana increase was not discovered until 2002 (Phillips et al. 2002); thus, there was no liana-nutrient deposition hypothesis to test until it was formulated much later (Schnitzer et al. 2011, Asner and Martin 2015). We measured stem diameters, mapped stem locations, identified to species, and assigned unique tag numbers for all lianas ≥5-cm diameter rooted in each $40 \times 40 \ m^2$ experimental plot and for all lianas ≥1-cm diameter rooted in the center 20×30 m section of plot. We included both liana individuals as well "clonal" liana stems—those that were still attached to another stem, but that had their own separate rooting location (Schnitzer et al. 2012). In the second census, we remeasured all of the stems that were present in 2013 and quantified rates of liana growth, mortality, and recruitment. Our methods for the liana censuses follow liana-specific protocols used in other large-scale studies (Schnitzer et al. 2012).

We scaled the liana density, basal area, and recruitment data to 1 ha to make our data comparable with other studies. During the 2018 census, we were unable to measure a small proportion of the stems (2.7%) because of the presence of Africanized bees or heavy decaying vegetation from recently fallen trees. Half of the unmeasured stems (65 individuals) were spread across one-third of the plots and were found in nearly all treatments, and the other half (64 individuals) were in a single plot (Plot 30, +P). We accounted for these sampling issues by omitting the 5×5 m subplots where the unmeasured stems were located from all analyses and scaling plots with omitted 5×5 m subplots to 1 ha (for liana density, basal area, and recruitment). For calculations of mortality rate, relative growth rate, and rarefied richness, we omitted unmeasured stems and did not rescale the data, because these variables are independent of area.

Data analysis

We quantified liana density, basal area, and species richness in 2013 and 2018, the change in these variables, as well as liana growth, recruitment, and mortality rates between 2013 and 2018. We calculated liana recruitment rate as the number of new stems per hectare per year. Relative growth rate of each individual was calculated as $RGR = \log(DBH_{2018} - DBH_{2013})/5$, where 5 is the number of years between censuses. We calculated annual mortality rate for all stems present in the 2013 and 2018 censuses as $m = 1 - (1 - (N_{2013} - N_{2018})/N_{2013})^{1/5}$, which can be simplified to $m = 1 - (N_{2018}/N_{2013})^{1/5}$, where N_{2013} corresponds to the number of lianas present in 2013 and N_{2018} corresponds to the number of lianas that had survived until the 2018 census (Sheil et al. 1995). We rarefied species richness to the lowest number of stems at the plot level to control for the positive relationship between liana density and diversity.

We used incomplete-block, factorial analyses of variance (ANOVA) to evaluate the effects of nutrient addition on liana density, basal area, and rarefied species richness in 2018 and on relative growth rates, recruitment, and mortality between 2013 and 2018. The ANOVA included main effects for N, P, and K, their two-way interactions, and spatial terms for blocks nested within replicates (follows Wright et al. 2018). We used repeated-measures incomplete-block, factorial ANOVAs to evaluate the effects of nutrient addition on changes in density, basal area, and rarefied richness between 2013 and 2018. The repeated-measures variable was census year, with two levels. We used Bartlett's test to evaluate the homogeneity of variance of residuals for each ANOVA and a power analysis that incorporated spatial variation associated with replicates and blocks to quantify statistical power. Analyses were conducted in R (R Development Core Team 2018).

Results

There were no significant responses to nutrient addition for any of the metrics that we examined. After 20 yr of nutrient addition, liana density, basal area, and rarefied species richness did not differ significantly among treatments nor between any treatment and the control (Fig. 1, Table 1). Likewise, relative growth, recruitment, and mortality rates from 2013 until 2018 did not differ significantly among nutrient treatments (Fig. 1, Table 1). Variation among plots was reasonably low, with coefficients of variation ranging from 0.21 to 0.62 for our primary response variables (liana density, basal area, and rarefied species richness). The power analysis demonstrated a 50% chance of detecting an effect size of 0.7 for P addition at the 5% significance level.

Between 2013 and 2018, we found a marginally significant increase in liana stem density ($P = 0.065$), a significant increase in liana basal area ($P = 0.025$), and a highly significant increase in rarefied richness
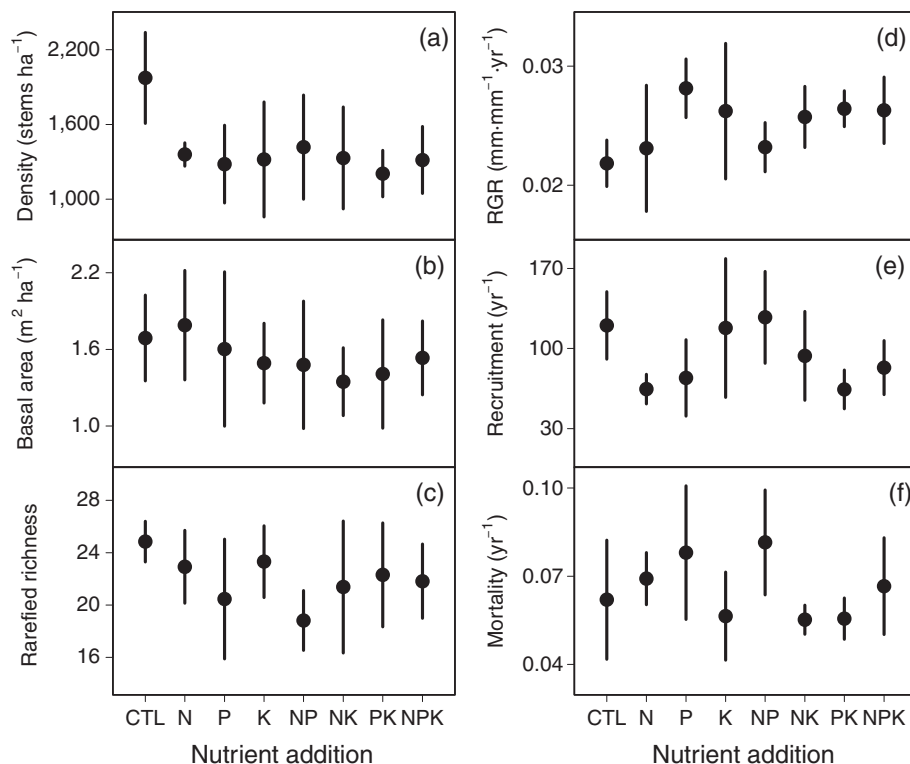
Fig. 1. Means and standard errors for (a) liana density, (b) basal area, (c) rarefied species richness, (d) relative growth rate, (e) recruitment rate, and (f) mortality rate after 20 yr of nutrient addition for the eight treatments of the factorial nitrogen (N), phosphorus (P), and potassium (K) experiment. The response of lianas did not differ signficantly in any of the treatments or the nonmanipulated control (CTL). All lianas ≥5-cm diameter that were rooted in the 40 × 40 m plots and all lianas ≥1-cm diameter that were rooted in the center 20 × 30 m of the plots were included. Density and basal area were standardized to a per-hectare basis. Rarefied richness was calculated as the number of species found from a random selection of liana individuals, with the number of individuals always equal to the number in the plot with the fewest lianas.

Table 1. Summary of incomplete-block factorial analyses of variance (ANOVA) examining effects of nutrient treatments on the density, basal area, and rarefied richness of lianas after 20 yr of nutrient addition, and relative growth rate, recruitment, and mortality between the 15th and 20th yr of nutrient addition.

Treatment	Density (ha^{-1})		Basal area (m^2/ha)		Rarefied richness		Relative growth rate		Mortality rate		Recruitment rate	
	$F_{1,18}$	P	$F_{1,18}$	P	$F_{1,18}$	P	$F_{1,18}$	P	$F_{1,18}$	P	$F_{1,18}$	P
N	0.173	0.682	0.002	0.968	0.470	0.502	0.339	0.568	0.300	0.591	0.008	0.929
P	0.796	0.384	0.088	0.770	1.078	0.313	0.935	0.346	1.087	0.311	0.289	0.598
K	1.016	0.327	0.617	0.442	0.041	0.841	1.287	0.271	2.320	0.145	0.097	0.759
N:P	0.983	0.335	0.002	0.962	0.040	0.844	0.627	0.439	0.053	0.821	3.013	0.099
N:K	0.490	0.493	0.000	0.997	0.017	0.897	0.172	0.683	0.000	0.984	0.001	0.977
P:K	0.346	0.564	0.251	0.622	0.820	0.377	0.581	0.456	0.227	0.640	0.854	0.368

Note: The ANOVA model included main effects for nitrogen (N), phosphorus (P), and potassium (K) and their two-way interactions. The eight treatments were replicated four times. There were no significant differences among any of the treatments for any of the response variables.

($P = 0.002$; Fig. 2, Table 2). During this period, mean liana density increased 8.0% from 1,492 ha^{-1} (±96) to 1,612 ha^{-1} (±112). Mean liana basal area increased 7.2% from 2.49 m^2/ha (±0.23) in 2013 to 2.67 m^2/ha (±0.26) in 2018. Mean liana rarefied richness increased 12.6% from 19.5 per plot (±0.75) in 2013 to 22.0 per plot (±0.97) in 2018. The annual increase in liana density, basal area, and richness was 1.6%, 1.4%, and 2.4%, respectively (Fig. 2). These data were based on a total of 3,967 liana stems comprising 84 species across the two
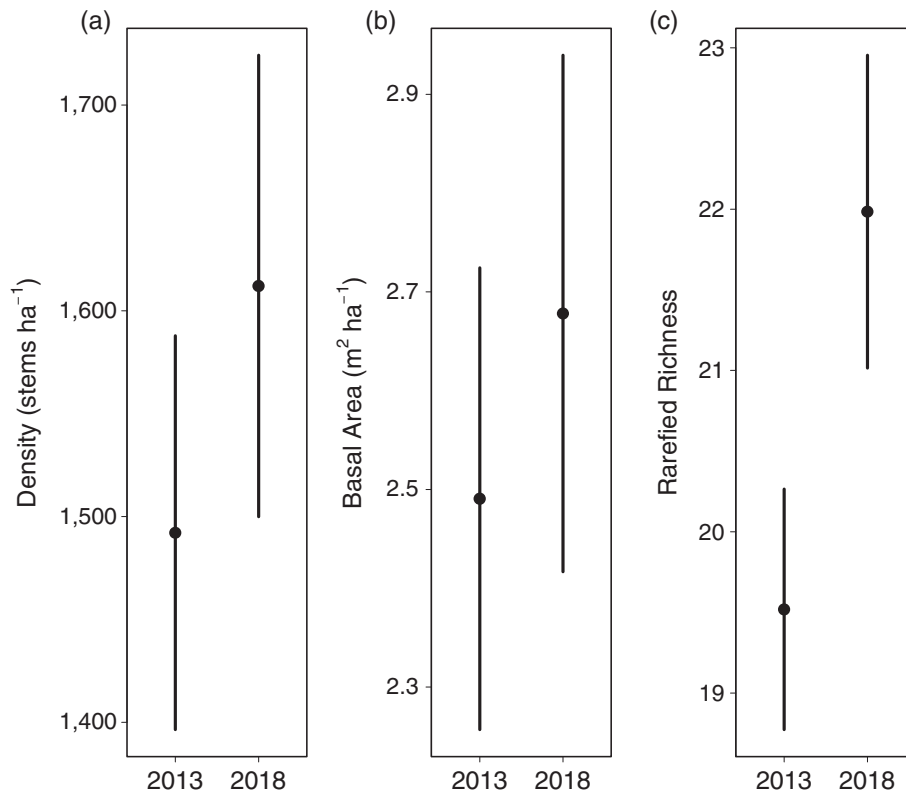
Fig. 2. Means and standard errors for the change in (a) liana density, (b) basal area, and (c) rarefied species richness from Years 15 to 20 (2013 to 2018) in a 32-plot factorial nitrogen, phosphorus, and potassium experiment. All lianas ≥5-cm diameter that were rooted in the 40 × 40 m plots and all lianas ≥1-cm diameter that were rooted in the center 20 × 30 m of the plots were included in this analysis. Liana density, basal area, and rarefied richness increased between 2013 and 2018 (Table 2; $P = 0.065$, $P = 0.025$ and $P = 0.0024$, respectively).

censuses. The five most abundant liana species (in 2018) comprised one-third of all of the rooted stems: *Doliocarpus dentatus* (Dilleniaceae) (349 stems), *Maripa panamensis* (Covolvulaceae) (217), *Combretum laxum* (Combretaceae) (207), *Prionostemma aspera* (Celastraceae) (164), and *Banisteriopsis cornifolia* (Malpighiaceae) (131).

DISCUSSION

The increase in liana density and basal area on Gigante Peninsula is consistent with liana increases in other tropical forests, and this study adds to growing evidence that liana density and BA are increasing in neotropical forests (Phillips et al. 2002, Schnitzer and Bongers 2011, Schnitzer 2015). The 1.6% per year increase in liana density on Gigante Peninsula was higher than the 1% per year increase reported for an old-growth Amazonian forest by Laurance et al. (2014), but lower than the increase in liana density on the nearby Barro Colorado Island (BCI), Panama, from 2007 to 2017 (S. A. Schnitzer, *unpublished data*). The 1.4% increase in liana BA on Gigante Peninsula was also

intermediate between a relatively low basal area increase in the Amazon (0.32%; Laurance et al. 2014) and a larger recent increase on BCI (S. A. Schnitzer, *unpublished data*). The increase in liana density and BA on the Gigante Peninsula were both less than the increases documented by Phillips et al. (2002), who reported that the density and basal area of large lianas (>10 cm diameter) increased by 4.0% per year and by 4.6% per year, respectively, across 28 long-term plots in South America. Nonetheless, increases of 1.6 and 1.4% per year are high and indicate that lianas are increasing at similar rates on the Gigante Peninsula and other old-growth neotropical forests.

Nutrient deposition is an unlikely explanation for increasing lianas in neotropical forests

Based on our findings, increasing nutrient deposition is not a likely candidate to explain observed increases in liana density, biomass, and productivity. After 20 yr of addition of nitrogen, phosphorus, and potassium, lianas had not responded significantly to any of the added nutrients, alone or in combination. If nutrient deposition

TABLE 2. Summary of repeated-measures incomplete-block factorial analyses of variance (ANOVA) examining effects of nutrient treatments on change in density, basal area, and rarefied richness between the 15th and 20th yr of nutrient addition. Liana basal area and rarefied richness both increased significantly between 2013 and 2018 (P-values italicized and bold); the increase in liana density between 2013 adn 2018 was marginally significant (italicized, non-bold P-values).

Treatment	Density (ha^{-1})		Basal area (m^2/ha)		Rarefied richness	
	$F_{1,18}$	P	$F_{1,18}$	P	$F_{1,18}$	P
Between-subjects or between-plot effects						
N	0.009	0.925	0.001	0.980	0.256	0.619
P	0.308	0.586	0.619	0.441	1.592	0.223
K	2.206	0.155	2.267	0.149	0.007	0.935
N:P	0.346	0.563	0.347	0.563	0.108	0.746
N:K	0.295	0.594	0.237	0.632	0.000	0.987
P:K	1.064	0.316	0.059	0.810	1.669	0.209
Within-subjects or within-plot effects						
Year	3.850	*0.065*	**5.984**	***0.025***	**12.506**	***0.0024***
N:year	0.055	0.817	0.105	0.749	0.760	0.394
P:year	0.140	0.712	0.361	0.555	0.005	0.946
K:year	0.901	0.355	2.540	0.128	0.713	0.409
N:P:year	1.268	0.275	0.099	0.757	2.113	0.163
N:K:year	0.090	0.768	0.076	0.786	0.135	0.718
P:K:year	1.661	0.213	0.773	0.391	0.204	0.523

Note: The ANOVA model included main effects for nitrogen (N), phosphorus (P), and potassium (K) and their two-way interactions with repeated measures on census year. The eight treatments were replicated four times. There were no significant differences among any of the nutrient treatments for any of the response variables. The within-plot effect of year revealed a marginally significant increase in liana density and significant increases in liana basal area and rarefied richness between 2013 and 2018.

had contributed to the increasing importance of lianas in neotropical forests (see Introduction), we would have expected 20 yr of intensive nutrient addition to cause detectable responses in the liana community. Further, if nutrients had been a driver of liana increases, we would have detected changes in liana density, basal area, or species richness from Years 15–20 of nutrient addition, which is when we had anticipated the strongest whole-plant and stand-level responses.

Nutrients limit many tropical forest plants (Wright 2019); however, after 20 yr of nutrient limitation in our plots, we have no evidence that nutrients limit the stand-level density, basal area, and demography of lianas. In this experiment, phosphorus addition increased photo-synthetic performance similarly in both tree and liana seedlings (Pasquini et al. 2015). In a meta-analysis of 48 nutrient-addition experiments conducted in tropical forests, nutrient addition increased tissue nutrient concentrations in trees, fine litter production, and, to a lesser extent, plant growth (Wright 2019). However, tree growth rates (Wright et al. 2018) and liana stem density, basal area, recruitment, growth, mortality, and richness (this study) have not responded to nutrient addition in our experiment.

Observational studies also indicate that soil nutrients are not a strong determinant of liana stem density, basal area, and distribution. On the Barro Colorado Island 50-ha plot in Panama), Dalling et al. (2012) found little evidence that the distribution of liana species varied with the availability of soil nutrients or soil chemistry. In the same 50-ha plot, Ledo and Schnitzer

(2014) reported that habitat type, which combined edaphic and topographical variables (e.g., elevation, slope, curvature, and aspect), did not explain liana distribution or abundance. Because lianas did not respond to aggressive nutrient addition in this study, and previous studies have not found a strong response of lianas to soil chemistry and habitat type (Dalling et al. 2012, Estrada-Villegas et al. 2020), it is unlikely that nutrient deposition is a strong explanatory factor for either the distribution of lianas or the increase of lianas in this and in other tropical forests with similar soil-nutrient levels.

Alternative explanations for increasing lianas in tropical forests

Alternative hypotheses to explain increasing lianas in neotropical forests include elevated atmospheric CO_2, hunting pressure, drought frequency and severity, and disturbance from tree mortality. Several experimental studies provide evidence suggesting that elevated CO_2 contributes to higher physiological performance and growth of lianas, particularly for temperate lianas (Manzanedo et al. 2018). For example, *Hedera helix* (English ivy) responded strongly to elevated CO_2, particularly in the low-light forest understory (Zotz et al. 2006), which may explain its increase in many temperate forests. In a CO_2 enrichment experiment, the growth rate of *Toxicodendron radicans* (poison ivy), was significantly higher at elevated CO_2 than ambient CO_2, and the biomass increase of *T. radicans* under elevated CO_2 was three- to

nearly five-times higher than that of other woody plants (Mohan et al. 2006). However, it remains unclear whether *T. radicans* is actually increasing in temperate forests (Londré and Schnitzer 2006) and, in this case, there may be a disconnect between experimental and in situ observational findings (Schnitzer et al. 2008).

Most previous experimental studies on the response of lianas to elevated CO_2 excluded trees, and thus they could not determine whether elevated CO_2 favored lianas over trees. In a more recent experiment in central Panama, Marvin et al. (2015) augmented CO_2 and found that both liana and tree growth was higher in elevated CO_2 compared to ambient CO_2 controls. Lianas did not, however, respond more strongly to elevated CO_2 than co-occurring trees, indicating that elevated atmospheric CO_2 does not favor lianas over trees. Similarly, phosphorus addition in our experiment increased seedling photosynthetic responses, but this effect did not differ between trees and liana (Pasquini et al. 2015).

If elevated CO_2 was the primary determinant of the increase in liana abundance, we would expect to find a uniform increase in lianas across tropical forests worldwide, since CO_2 emissions mix rapidly in the atmosphere. Increasing liana density, biomass, or productivity have been reported in neotropical forests (Schnitzer and Bongers 2011, Schnitzer 2015) and in one forest in central Asia (India; Pandian and Parthasarathy 2016); however, a second study from Asia reported no change in lianas (measured as tree infestation levels; Wright et al. 2015) and studies from Africa have reported decreases in liana density (e.g., Bongers et al. 2020). Although additional studies are necessary to determine the role of rising atmospheric CO_2 on liana-specific responses, evidence for the hypothesis that CO_2 is a strong determinant for increasing neotropical lianas is not yet compelling.

Increased hunting of seed-dispersing animals could explain why lianas have increased more strongly in neotropical forests than in Old World tropical forests. The seeds of more than 80% of neotropical tree species are dispersed by frugivores, whereas the seeds of 63% of neotropical liana species are dispersed by wind (Muller-Landau and Hardesty 2005). Hunters reduce frugivore numbers and thus they reduce seed dispersal by frugivores (Markl et al. 2012); however, hunting does not affect seed dispersal by wind. By contrast, in the Old World tropics, the seeds of the great majority of both tree and liana species are dispersed by frugivores (Wright et al. 2015). Therefore, in Old World tropical forests the loss of frugivores due to poaching is unlikely to affect the relative success of lianas over trees, which is consistent with the lack of evidence for increasing lianas in most Old World tropical forests (but see Pandian and Parthasarathy 2016). The hunting hypothesis cannot, however, explain recent observation on the Barro Colorado Island, Panama (BCI) 50-ha plot, where hunters have been excluded since 1987, yet liana stem density and basal area increased substantially from 2007 to 2017 (S. A. Schnitzer, *unpublished data*; see also Wright et al. 2004, Umaña et al. 2020).

Increasing intensity and severity of drought may also explain increasing neotropical liana abundance. Many tropical forests are experiencing increasing duration and intensity of droughts, including longer and more intense dry seasons (Dai 2013). Lianas may capitalize on the high solar radiation associated with drought-like conditions by growing more during arid periods, which could increase their abundance (Schnitzer 2018). Indeed, in a 5-yr study on more than 650 canopy lianas and 1,100 canopy trees in central Panama, lianas grew most during the dry season, whereas trees grew most during the wet season (Schnitzer and van der Heijden 2019). However, increasing drought does not appear to explain liana increases in central Panama, where annual rainfall has increased since the 1980s (S. Paton, *unpublished data*).

Elevated disturbance may explain increasing liana abundance in neotropical forests. Tree mortality, and thus disturbance, has increased substantially in tropical forests over the past 40 yr (McDowell et al. 2018). Tree mortality increases with more frequent violent storms that cause windthrows and lightning strikes, as well as with more severe and frequent droughts (Choat et al. 2018, McDowell et al. 2018, Yanoviak et al. 2020). Lianas capitalize on disturbed areas in tropical forests via enhanced seed arrival, recruitment, establishment, and growth, and liana density and diversity are commonly much higher in treefall gaps than in undisturbed forest (Schnitzer and Bongers 2002, Schnitzer 2018). For example, on the 50-ha plot on BCI, disturbances associated with tree falls explained the abundance and distribution of most liana species (Dalling et al. 2012). Disturbance may promote liana abundance because disturbed areas have high light availability, which provide a regeneration niche for lianas (Ledo and Schnitzer 2014, Schnitzer 2018). Tree mortality decreased from 1982 to 1990 but has increased only modestly since 1990 (Condit et al. 2017); thus, disturbance from significantly elevated tree mortality does not appear to explain the ongoing increase in lianas on the BCI 50-ha plot.

In conclusion, this study represents the first large-scale, long-term experimental test of the role of nutrients as an explanation for liana distribution and increasing abundance in neotropical forests. We found that lianas were increasing in our plots, but there was no support for the hypothesis that nutrient deposition contributes to observed liana increases. Our findings are consistent with observational studies (Dalling et al. 2012, Ledo and Schnitzer 2014, Estrada-Villegas et al. 2020), which reported that soil nutrients and soil chemistry were poor predictors of liana abundance and distribution. Therefore, the distribution of lianas and their increase in neotropical forests are likely not the result of elevated nutrient deposition. Other potential causes for the increase in liana density and biomass, such as elevated CO_2, poaching, drought, and forest disturbance are also not yet supported and need more rigorous testing.

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