

Long-term changes in liana abundance and forest dynamics in undisturbed Amazonian forests

WILLIAM F. LAURANCE,^{1,5} ANA S. ANDRADE,² AINHOA MAGRACH,¹ JOSÉ L. C. CAMARGO,² JEFFERSON J. VALSKO,²
MASON CAMPBELL,¹ PHILIP M. FEARNside,³ WILL EDWARDS,¹ THOMAS E. LOVEJOY,^{2,4} AND SUSAN G. LAURANCE¹

¹Centre for Tropical Environmental and Sustainability Science and School of Marine and Tropical Biology, James Cook University, Cairns, Queensland 4878 Australia

²Biological Dynamics of Forest Fragments Project, National Institute for Amazonian Research (INPA) and Smithsonian Tropical Research Institute, Manaus, Amazonas 69060 000 Brazil

³Department of Ecology, National Institute for Amazonian Research (INPA), Manaus, Amazonas 69060 000 Brazil

⁴Department of Environmental Science and Policy, George Mason University, Fairfax, Virginia 22030 USA

Abstract. Lianas (climbing woody vines) are important structural parasites of tropical trees and may be increasing in abundance in response to global-change drivers. We assessed long-term (~14-year) changes in liana abundance and forest dynamics within 36 1-ha permanent plots spanning ~600 km² of undisturbed rainforest in central Amazonia. Within each plot, we counted each liana stem (≥ 2 cm diameter) and measured its diameter at 1.3 m height, and then used these data to estimate liana aboveground biomass. An initial liana survey was completed in 1997–1999 and then repeated in 2012, using identical methods.

Liana abundance in the plots increased by an average of $1.00\% \pm 0.88\%$ per year, leading to a highly significant ($t = 6.58$, $df = 35$, $P < 0.00001$) increase in liana stem numbers. Liana biomass rose more slowly over time ($0.32\% \pm 1.37\%$ per year) and the mean difference between the two sampling intervals was nonsignificant ($t = 1.46$, $df = 35$, $P = 0.15$; paired t tests). Liana size distributions shifted significantly ($\chi^2 = 191$, $df = 8$, $P < 0.0001$; Chi-square test for independence) between censuses, mainly as a result of a nearly 40% increase in the number of smaller (2–3 cm diameter) lianas, suggesting that lianas recruited rapidly during the study.

We used long-term data on rainfall and forest dynamics from our study site to test hypotheses about potential drivers of change in liana communities. Lianas generally increase with rainfall seasonality, but we found no significant trends over time (1997–2012) in five rainfall parameters (total annual rainfall, dry-season rainfall, wet-season rainfall, number of very dry months, CV of monthly rainfall). However, rates of tree mortality and recruitment have increased significantly over time in our plots, and general linear mixed-effect models suggested that lianas were more abundant at sites with higher tree mortality and flatter topography. Rising concentrations of atmospheric CO₂, which may stimulate liana growth, might also have promoted liana increases.

Our findings clearly support the view that lianas are increasing in abundance in old-growth tropical forests, possibly in response to accelerating forest dynamics and rising CO₂ concentrations. The aboveground biomass of trees was lowest in plots with abundant lianas, suggesting that lianas could reduce forest carbon storage and potentially alter forest dynamics if they continue to proliferate.

Key words: Amazon; biomass; CO₂ fertilization; carbon storage; forest disturbance; forest dynamics; lianas; tree infestation; tree mortality; undisturbed forest; woody vines.

INTRODUCTION

Lianas (climbing woody vines) are a major feature of tropical rainforests. They constitute 10–45% of all woody plants and species (Schnitzer and Bongers 2002) and produce up to 40% of the leaves in the forest (Kato et al. 1978, Putz 1983). Occasionally growing to >50 cm in diameter and several hundred meters in

length (Schnitzer et al. 2012), lianas exploit trees for physical support in order to reach the forest canopy. By creating structural stresses on trees and competing for light, nutrients, and water, liana infestations can reduce tree growth, fecundity, survival, and recruitment (Putz 1984, Stevens 1987, Schnitzer et al. 2000, Schnitzer and Carson 2010, Yorke et al. 2013). As a result, they can have a considerable impact on forest dynamics (see Plate 1), tree species composition, and carbon storage (Schnitzer and Bongers 2002, 2011, Körner 2004).

Most liana species are light loving and increase markedly in abundance in forests disturbed by wind-

Manuscript received 13 August 2013; revised 15 November 2013; accepted 3 December 2013. Corresponding Editor: J. B. Yavitt.

⁵ E-mail: bill.laurance@jcu.edu.au

storms (Webb 1958), logging (Appanah and Putz 1984), and habitat fragmentation (Laurance et al. 2001). They may also be increasing even in undisturbed forests. Liana abundances have been reported to have risen over time in old-growth forests in western Amazonia (Phillips et al. 2002, Foster et al. 2008), the Guianas (Chave et al. 2008), and Central America (Wright et al. 2004, Ingwell et al. 2010, Schnitzer et al. 2012, Yorke et al. 2013). Liana seedlings were also observed to proliferate in central Amazonia (by ~500% over 6.5 years), although this involved the colonization of small experimental clearings (Benítez-Malvido and Martínez-Ramos 2003) where liana recruitment might be favored.

Three main hypotheses have been proposed to explain the apparent increase in liana abundances in undisturbed old-growth forests (Schnitzer and Bongers 2011). First, seasonal droughts may be increasing in some tropical regions, such as the southern Amazon (Fu et al. 2013), possibly as a result of regional or global climate change (Lewis et al. 2011, Brodie et al. 2012). Droughts would likely benefit lianas (Ingwell et al. 2010, Enquist and Enquist 2011), which are more resilient and grow faster than do trees under dry conditions (Schnitzer 2005, Cai et al. 2009). Second, elevated atmospheric CO₂ may increase liana growth and fecundity (Hättenschwiler and Körner 2003, Mohan et al. 2006, Körner 2009), especially in the deep shade of the forest understory (Granados and Körner 2002, Zotz et al. 2006). Finally, rates of tree mortality and turnover appear to be increasing in many tropical forests, possibly because forests are becoming more productive and competitive as a result of rising CO₂ fertilization (Phillips and Gentry 1994, Laurance et al. 2004, 2009, Lewis et al. 2004a). Such elevated forest dynamics would produce more treefall gaps, where lianas proliferate in stem number and diversity (Putz 1984, Schnitzer and Carson 2001, Dalling et al. 2012, Schnitzer et al. 2012). These three mechanisms are not mutually exclusive and might operate in concert or even synergistically (Schnitzer and Bongers 2011).

Here we assessed long-term (~14-year) changes in liana abundance and biomass in undisturbed, old-growth forests of central Amazonia, which overlay nutrient-poor soils typical of much of the Amazon basin (Bravard and Righi 1989). Our network of 36 permanent 1-ha plots spans an extensive geographic area (~600 km²) and also provides long-term data on forest dynamics, tree-stand attributes, topography, and soil features (e.g., Laurance et al. 1997, 1999, 2000, 2006). When combined with local weather records, these data allow us to test leading hypotheses about the potential drivers and ecological consequences of changing liana abundance.

METHODS

Study area

This study was conducted in old-growth rainforests of the Biological Dynamics of Forest Fragments Project

(28°30' S, 60° W), a large-scale experimental study of habitat fragmentation located 70 km north of Manaus, Brazil (Lovejoy et al. 1986). The 36 permanent, 1-ha plots in the study span an area of about 15 × 40 km and range from 60 to 100 m elevation. All plots were located ≥150 m from the nearest forest–pasture margin to minimize edge effects (Laurance et al. 2002, 2011) and exhibited no evidence of anthropogenic disturbances such as selective logging, fires, or past agriculture (Laurance et al. 2004, 2005).

The forests of the study area are among the most diverse in the world (averaging ~260 tree species of ≥10 cm diameter at breast height [dbh]/ha) with a typical canopy height of 37–40 m (Laurance et al. 2010). The dominant soils in the study area are xanthic ferralsols (Fearnside and Leal Filho 2001), which are heavily weathered and nutrient poor (Beinroth 1975). In this region, clay-rich plateaus are frequently dissected by steep stream gullies, which have higher sand contents and lower concentrations of most soil nutrients (Chauvel et al. 1987). Rainfall ranges from 1900 to 3500 mm annually with a moderately strong dry season from June to October (Laurance 2001).

Data collected

The 36 permanent plots we studied were established in the early to mid 1980s, with an initial focus on tree-community dynamics and forest-carbon storage (Laurance et al. 1997, 1998, 2006a, b). Within each plot, all trees (≥10 cm dbh) were measured at 1.3 m height or above any buttresses, mapped, and tagged, with sterile or fertile material collected to facilitate species identification. Each plot was recensused at a nominal interval of ~5 years to record any dead, damaged, or newly recruited trees, with the most recent tree census in 2009. Annualized rates of tree mortality were estimated using a logarithmic model (Sheil et al. 1995), corrected for variation in census interval (Lewis et al. 2004b). The aboveground dry biomass (AGBM) of live trees was estimated for each plot and census using an allometric formula based on destructively sampling 315 trees in nearby rainforests (Chambers et al. 2001).

Liana data in all but three of our plots were initially collected in 1997–1999 (Laurance et al. 2001), with the remaining three plots censused for lianas in early 2001. All plots were resampled, using identical methods, in 2012, for a mean (±SD) resampling interval of 13.6 ± 0.7 years. Within each plot, all lianas (≥2 cm diameter) were counted and measured at 1.3 m height, following established protocols for enumerating liana stems (Putz 1984, Schnitzer et al. 2006). As is typical, no attempt was made to distinguish liana ramets and genets. Liana stems were not individually tagged during the initial survey, and thus, estimates of liana recruitment and mortality could not be generated. Estimates of liana aboveground dry biomass (AGBM) were derived with an allometric model using liana stem diameter data (*D*)



PLATE 1. Lianas can form dense tangles that reduce tree survival, growth, and regeneration in tropical forests. Photo credit: W. F. Laurance.

from many different studies (Schnitzer et al. 2006), as follows:

$$\text{AGMB} = \exp[-1.484 + 2.657\ln(D)]. \quad (1)$$

The only exception from established protocols was that in 1997–1999 we measured the diameter of noncircular liana stems (which constituted just 1.4% of all stems) with a dbh tape, rather than averaging their length and width, as is now recommended (Schnitzer et al. 2006). For the sake of consistency, we retained this method in 2012, but found it had little impact on our estimates of liana ABGM (using 2012 data, ABGM values for each plot calculated using the two methods differed by just 0.5%, on average).

Mean slope was determined for each plot with a clinometer, by dividing the plot into 25 subplots (each 20 × 20 m), determining the maximum slope within each subplot, and then averaging these values. In our study area, mean slope is a good proxy for soil texture and nutrient status; the major gradient is between clay-rich soils in flatter areas with higher C, N, cation exchange capacity, and exchangeable bases, and sandy, nutrient-starved soils in steeper sites with greater aluminum toxicity (Laurance et al. 1999, 2001, 2010).

Monthly rainfall data were collected from the Brazilian National Institute for Meteorology weather station

in Manaus, from 1997 to 2012 (*available online*).⁶ These data were used to generate five annual weather parameters: total rainfall, dry-season rainfall (May–October), wet-season rainfall (November–April), the coefficient of variation (CV) in monthly rainfall, and the number of “very dry” months (those with <50 mm of rainfall). Monthly rainfall in Manaus and the study area are strongly correlated, but the latter tends to be somewhat wetter on average, especially in the dry season (Laurance 2001). Daily rainfall data were recorded in the study area from 1988 to 1998, but records have been inconsistent since then.

Data analysis

We assessed changes in liana abundance and biomass over time in our 36 plots using paired *t* tests. Data were log-transformed prior to analysis if differences between paired samples deviated significantly from normality. Changes over time in liana size-distributions were assessed with a Chi-square test for independence.

We tested effects of three possible predictors on liana abundance in 1997–1999 and in 2012. Our possible predictors were (1) mean number of trees per plot, (2) mean rate of tree turnover (the average of annualized rates of tree mortality and recruitment, a commonly used index of forest dynamics; Phillips and Gentry 1994), and (3) mean slope of the plot. To do this, we fitted general linear mixed models (GLMM) with Gaussian error distributions and identity link functions, using function *glmmadmb* in R's *glmmADMB* package (Bolker et al. 2012). Plots in the study area occur in three relatively discrete blocks (Laurance et al. 1998), and hence, block was included as a random variable to account for the possible nonindependence of samples within the same block. All variables were included in the general model because, in previous tests for collinearity, the variance-inflation factors for all variables were <3 (Zuur et al. 2009). Logarithmic and arcsine square-root transformations were used to improve the linear fits of tree mortality and slope data, respectively. All potential predictors were standardized prior to analysis so their effect sizes could be compared directly.

RESULTS

Liana abundance and size distributions

In our 36 plots, we recorded a total of 13 544 lianas in 1997–1999, and 15 549 lianas in 2012. The increase in mean (\pm SD) liana abundance over time (Fig. 1), from 376 ± 107 (range 200–637) to 428 ± 118 (range 224–682) stems/ha, was highly significant ($t = 6.58$, $df = 35$, $P < 0.00001$; paired *t* test with log-transformed data). On average, liana stems increased on each plot by $1.00\% \pm 0.88\%$ per year.

The size distributions of lianas (Fig. 2) exhibited a highly significant shift over time ($\chi^2 = 190.9$, $df = 8$, $P <$

⁶ <http://www.inmet.gov.br>

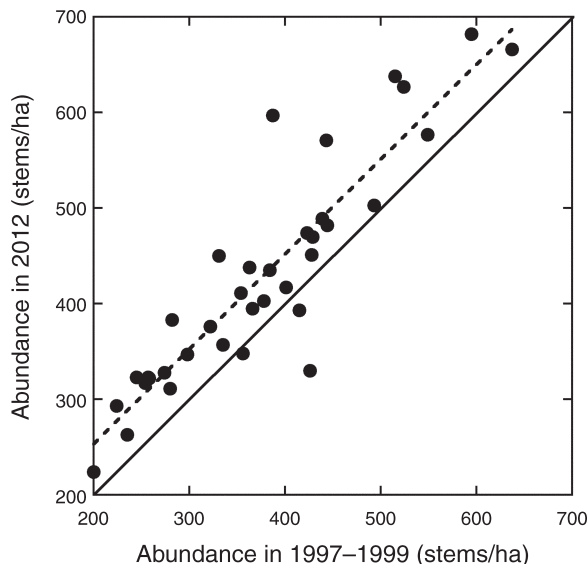


FIG. 1. Comparison of liana abundance (stems \geq 2 cm diameter) between 1997–1999 and 2012 for 36 1-ha plots in undisturbed Amazonian forests. The solid line shows $Y = X$, whereas the dotted line shows a fitted linear regression between liana abundances during the two time periods.

0.00001; Chi-square test for independence). This shift mainly resulted from a nearly 40% increase in the number of small (2–3 cm diameter) lianas, from 136 ± 43 stems/ha in 1997–1999 to 190 ± 56 stems/ha in 2012. Lianas in most of the larger size classes also increased over time, but the proportional differences were mostly minor (Fig. 2).

Liana biomass

The estimated mean biomass of lianas also rose over time, from 7.7 ± 2.3 Mg/ha in 1997–1999 to 8.0 ± 2.2 Mg/ha in 2012, but this difference was nonsignificant (t

$= 1.46$, $df = 35$, $P = 0.15$; paired t test with log-transformed biomass data). In annualized terms, biomass increased by $0.32\% \pm 1.37\%$ per year. Results were similar for liana basal area, which rose from 0.717 ± 0.194 to 0.748 ± 0.186 m²/ha, on average, between 1997–1999 and 2012. This difference was marginally nonsignificant ($t = 1.90$, $df = 35$, $P = 0.065$; paired t test).

Estimates of liana biomass for each plot were heavily influenced by a few large lianas. In 2012, large (>10 cm diameter) lianas constituted just 2.7% of all recorded stems, but 40.9% of estimated biomass. The number of large lianas per plot explained much of the variation in liana biomass ($F_{1,34} = 53.78$, $R^2 = 61.3\%$, $P < 0.0001$; linear regression). Patterns were similar in 1997–1999.

Plots with many large lianas in 1997–1999 tended to have many large lianas in 2012 ($r = 0.729$, $P < 0.0001$). Likewise, plots with many smaller (≤ 10 cm) lianas in 1997–1999 had many smaller lianas in 2012 ($r = 0.898$, $P < 0.0001$). There was no significant correlation between the number of large and smaller lianas per plot in either 1997–1999 ($r = 0.149$, $P = 0.39$) or 2012 ($r = 0.055$, $P = 0.75$). However, in both 1997–1999 ($r = -0.553$, $P = 0.0005$) and 2012 ($r = -0.509$, $P = 0.0015$), large lianas were relatively less frequent (comprising a smaller percentage of all liana stems) in plots with higher numbers of lianas (all Pearson correlations with $df = 34$).

Predicting liana abundance

The GLMM analyses suggested that two variables, mean slope and our index of forest dynamics (mean tree-turnover rate), were moderately useful predictors of liana abundance in 1997–1999 and again in 2012 (Table 1). Lianas were generally more abundant on flatter sites with greater forest dynamics. Effect sizes for the two predictors were similar in 1997–1999, whereas slope had a somewhat stronger influence on lianas in 2012.

Notably, forest dynamics have generally increased over time in our plots. Using available data for 33 of the

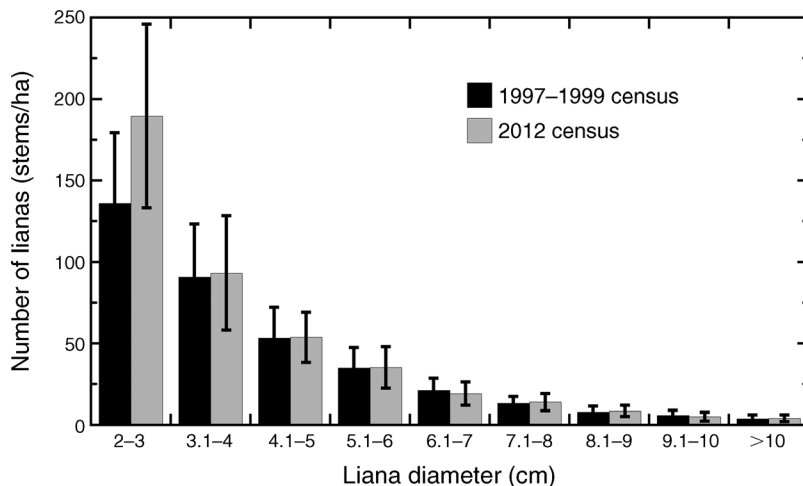


FIG. 2. Mean number (\pm SD) of liana stems in different diameter classes recorded within 36 1-ha plots in central Amazonia in 1997–1999 ($n = 13\ 544$) and 2012 ($n = 15\ 549$).

TABLE 1. Potential predictors of liana abundance in 1997–1999 and 2012 within 36 1-ha plots in undisturbed Amazonian forest, using general linear mixed-effects models.

Predictor	Estimate	SE	Z	P
Number of liana stems in 1997–1999				
Intercept	376.2	16.2	23.29	<0.0001
Tree turnover rate†	30.7	17.2	1.78	0.075
Number of tree stems	11.3	17.2	0.66	0.51
Slope‡	–33.2	16.8	–1.97	0.048
Number of liana stems in 2012				
Intercept	428.2	17.3	24.79	<0.0001
Tree turnover rate†	30.4	18.4	1.65	0.098
Number of tree stems	12.8	18.3	0.70	0.49
Slope‡	–47.7	18.0	–2.65	0.008

Note: The effect size of each predictor is proportional to the absolute value of its estimate value, with negative values indicating a negative slope.

† Data \log_{10} -transformed.

‡ Data arcsine square-root transformed.

plots, we contrasted mean mortality and recruitment rates of trees between two largely nonoverlapping intervals: the early-mid 1980s to late 1997, vs. early 1998 to late 2009 (Fig. 3). Tree mortality increased modestly but significantly over time ($t = 2.19$, $P = 0.036$), from $1.33\% \pm 0.64\%$ to $1.46\% \pm 0.36\%$ per year. Tree recruitment rose more markedly, from $1.15\% \pm 0.32\%$ to $1.46\% \pm 0.53\%$ per year, a highly significant difference ($t = 3.19$, $P = 0.0031$; paired t tests with $df = 32$ and log-transformed data).

Rainfall

We found no evidence of changing rainfall trends that might influence liana abundance. Using Pearson correlations between the year and annual weather variables from 1997 to 2012, there were no significant trends in total rainfall ($r = 0.158$, $P = 0.56$), dry-season rainfall ($r = -0.151$, $P = 0.58$), wet-season rainfall ($r = 0.253$, $P = 0.34$), the number of very dry months ($r = -0.236$, $P = 0.38$), and the CV of monthly rainfall ($r = -0.034$, $P = 0.90$). Analyses with Spearman rank correlations, which are insensitive to nonlinear trends, were similar.

DISCUSSION

Increasing liana abundance

Our large-scale study suggests that in central Amazonian forests, lianas are progressively increasing in abundance, at a mean rate of $\sim 1\%$ per year over the past 14 years (Fig. 1). The forests of our study area overlay heavily weathered, infertile soils, which typify much of the vast Amazon Basin. Our findings accord with several other studies, most of which are smaller scale or shorter term in nature, which suggest that lianas are increasing in old-growth Neotropical forests (Phillips et al. 2002, Benítez-Malvido and Martínez-Ramos 2003, Wright et al. 2004, Foster et al. 2008, Ingwell et al. 2010, Schnitzer et al. 2012, Yorke et al. 2013).

The proliferation of lianas we observed largely resulted from increases in smaller sized lianas (Fig. 2),

suggesting that liana recruitment was high during the course of our study (1997–2012). Most smaller (2–3 cm diameter) lianas have already reached the forest canopy (Kurzel et al. 2006), indicating that they are potentially important ecologically even at that limited size. Liana biomass rose only slightly (from an average of 7.7 to 8.0 Mg/ha) and was highly variable among plots as a result of the patchy distribution of large (≥ 10 cm diameter), heavy lianas. Our findings are consistent with those of Benítez-Malvido and Martínez-Ramos (2003), who observed a striking increase in numbers of liana seedlings ($\sim 500\%$ over 6.5 years) in our same study area. However, the degree to which their study reflects reality is uncertain, because it measured seedling recruitment within small (1 m^2), artificial clearings that might not reflect actual recruitment processes. Most lianas favor gap and edge environments and are adept at colonizing clearings, via both seed dispersal and especially clonal growth (Putz 1984, Schnitzer et al. 2000, 2012, Dalling et al. 2012, Yorke et al. 2013).

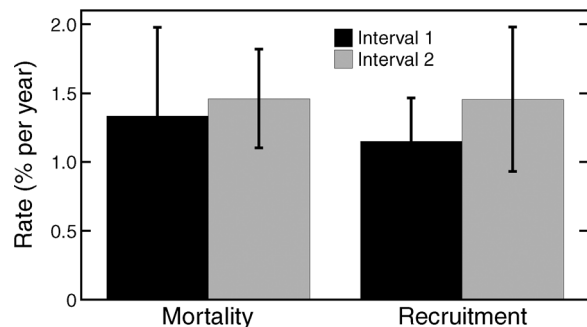


FIG. 3. Mean annualized rates (\pm SD) of tree mortality and recruitment in 33 1-ha plots in undisturbed Amazonian forests, contrasted between interval 1 (early to mid 1980s to late 1997) and interval 2 (early 1998 to late 2009). Rates are based on five to eight standardized censuses of trees (≥ 10 cm diameter at breast height) within each plot.

Potential drivers of liana increases

Lianas are known to increase at the expense of trees under conditions of increasing rainfall seasonality and declining total rainfall (Schnitzer and Bongers 2002, 2011). However, we found no evidence for any such trends during the course of our study (1997–2012), suggesting that the liana increases we observed did not result from changing weather conditions.

Our findings are, however, broadly consistent with the notion that lianas, which favor disturbed forests, might be increasing in response to accelerating forest dynamics. In our study area, lianas tended to be abundant in plots with high tree turnover (Table 1), and rates of tree mortality and recruitment have both increased significantly in recent decades (Fig. 3). Similar trends have recently been detected in a single 50-ha plot on Barro Colorado Island, Panama (Dalling et al. 2012, Schnitzer et al. 2012). These increases have several potential explanations (Laurance et al. 2004, 2009), including the possibility that rising concentrations of atmospheric CO₂ are fertilizing plants and thereby accelerating forest productivity and plant growth (Phillips and Gentry 1994, Lewis et al. 2004a). Accelerated growth, in turn, might be expected to increase plant competition and thereby lead to more rapid tree mortality and recruitment, as well as faster tree senescence. Notably, the large majority of tree genera in our study area have exhibited accelerating growth rates over time (Laurance et al. 2004), which suggests that forest productivity has indeed increased.

In addition, CO₂ increases might fertilize lianas to a greater extent than trees (Würth et al. 1998, Hätenschwiler and Körner 2003, Schnitzer and Bongers 2011), leading to liana increases. This difference might be attributable to the proportionately greater leaf area of lianas, which could allow them to fix more carbon and grow more rapidly than do trees under elevated CO₂ conditions (Cai et al. 2009). Additional attributes of lianas, such as their high photosynthetic rates, high N and P use efficiencies, and tolerance of drought stress, might also enhance their response to CO₂ enrichment beyond that experienced by trees (Zhu and Cao 2010). If CO₂ fertilization of lianas is marked, then it would presumably also translate into increased liana fecundity and recruitment, which could produce the major increase in smaller lianas observed in this study (Fig. 2). Notably, CO₂ concentrations rose rapidly during the course of our study, from 363 ppm in 1997 to 394 ppm in 2012 (Earth Systems Research Laboratory, *available online*).⁷

Implications of liana increases

Given their antagonistic relationships with trees, it has been suggested that increasing liana abundances could have a number of impacts on tropical forest communi-

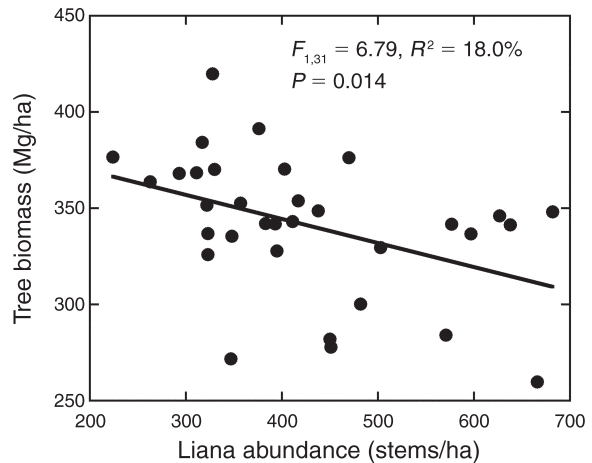


FIG. 4. Relationship between liana abundance in 2012 and mean aboveground tree biomass for 33 1-ha plots in undisturbed Amazonian forests.

ties. Tree species differ in their susceptibility to lianas, with slower growing, shade-tolerant species being particularly vulnerable and pioneer species far less so (Putz 1984, Ingwell et al. 2010, Schnitzer and Carson 2010). Lianas thus have the potential to alter the composition and dynamics of tree communities, especially where they are abundant (Appanah and Putz 1984, Putz 1984, Schnitzer and Bongers 2002, 2011).

Beyond this, lianas could potentially have a sizeable impact on forest carbon storage, by reducing tree growth and survival, especially for shade-tolerant species, which have high wood densities, and thus, high carbon storage (Laurance et al. 2001, 2006b, Körner 2004). For instance, in our old-growth forest plots, we found that lianas had a strong negative relationship with aboveground tree biomass (Fig. 4). It is difficult to separate cause and effect because lianas might either have suppressed tree biomass or have increased where extrinsic mortality events, such as droughts, windstorms, or disease outbreaks, had previously damaged forests. Nevertheless, these data clearly suggest that abundant lianas have the potential to reduce forest carbon storage, especially if they increase further in the future (Schnitzer and Bongers 2011, Fearnside 2013). In addition, lianas generally have low wood density and invariably invest far less in woody tissue than do trees (Putz 1984). Hence, even where hyper-abundant, lianas are unlikely to replace more than a small fraction of the tree biomass that they kill or suppress.

It has been assumed in recent studies that likely consequences of increasing atmospheric CO₂ concentrations on old-growth tropical forests will be increasing forest-carbon storage and drought resistance (Cox et al. 2013, Huntingford et al. 2013). However, the effects of proliferating lianas documented here and in other recent studies (see Ingwell et al. 2010, Schnitzer and Bongers 2011, Fearnside 2013) should temper the assumption

⁷ <http://www.esrl.noaa.gov/gmd/ccgg/trends/global.html>

that all potential effects of rising CO₂ will reduce emissions from these forests.

ACKNOWLEDGMENTS

We thank Stefan Schnitzer and two anonymous referees for commenting on the manuscript. Support was provided by the Conservation, Food and Health Foundation, Australian Research Council, U.S. National Science Foundation, NASA Long-term Biosphere-Atmosphere Experiment in the Amazon, A. W. Mellon Foundation, MacArthur Foundation, World Wildlife Fund-US, National Institute for Amazonian Research, and Smithsonian Institution. This is publication number 628 in the Biological Dynamics of Forest Fragments Project (BDFFP) technical series.

LITERATURE CITED

- Appanah, S., and F. E. Putz. 1984. Climber abundance in virgin dipterocarp forest and the effect of pre-felling climber cutting on logging damage. *Malaysian Forester* 47:335–342.
- Beinroth, F. H. 1975. Relationships between U.S. soil taxonomy, the Brazilian system, and FAO/UNESCO units. Pages 97–108 in E. Bornemisza and A. Alvarado, editors. *Soil management in tropical America*. North Carolina State University, Raleigh, North Carolina, USA.
- Benítez-Malvido, J., and M. Martínez-Ramos. 2003. Impact of forest fragmentation on understory plant species richness in Amazonia. *Conservation Biology* 17:389–400.
- Bolker, B., H. Skaug, A. Magnusson, and A. Nielsen. 2012. Getting started with the *glmmADMB* package. R Foundation for Statistical Computing, Vienna, Austria. <http://glmmadmb.r-forge.r-project.org/glmmADMB.pdf>
- Bravard, S., and D. Righi. 1989. Geochemical differences in an oxisol-spodosol toposequence of Amazonia Brazil. *Geoderma* 44:29–42.
- Brodie, J., E. Post, and W. F. Laurance. 2012. Climate change and tropical biodiversity: a new focus. *Trends in Ecology and Evolution* 23:145–150.
- Cai, Z.-Q., S. A. Schnitzer, and F. Bongers. 2009. Seasonal differences in leaf-level physiology give lianas a competitive advantage over trees in a tropical seasonal forest. *Oecologia* 161:25–33.
- Chambers, J. Q., J. Santos, R. J. Ribeiro, and N. Higuchi. 2001. Tree damage, allometric relationships, and above-ground net primary production in a tropical forest. *Forest Ecology and Management* 152:73–84.
- Chauvel, A., Y. Lucas, and R. Boulet. 1987. On the genesis of the soil mantle of the region of Manaus, Central Amazonia, Brazil. *Experientia* 43:234–240.
- Chave, J., J. Olivier, F. Bongers, P. Chatelet, P. M. Forget, P. van der Meer, N. Norden, B. Riera, and P. Charles-Dominique. 2008. Above-ground biomass and productivity in a rain forest of eastern South America. *Journal of Tropical Ecology* 24:355–366.
- Cox, P. M., D. Pearson, B. B. Booth, P. Friedlingstein, C. Huntingford, C. D. Jones, and C. M. Luke. 2013. Sensitivity of tropical carbon to climate change constrained by carbon dioxide variability. *Nature* 494:341–344.
- Dalling, J. W., S. A. Schnitzer, C. Baldeck, K. Harms, R. John, S. Mangan, E. Lobo, J. Yavitt, and S. P. Hubbell. 2012. Resource-based habitat associations in a neotropical liana community. *Journal of Ecology* 100:1174–1182.
- Enquist, B. J., and C. A. F. Enquist. 2011. Long-term change within a Neotropical forest: Assessing differential functional and floristic responses to drought and past disturbances. *Global Change Biology* 17:1408–1424.
- Fearnside, P. M. 2013. Vines, CO₂ and Amazon forest dieback. Nature Online Comment. <http://dx.doi.org/10.1038/nature11882>
- Fearnside, P. M., and N. Leal Filho. 2001. Soil and development in Amazonia: Lessons from the Biological Dynamics of Forest Fragments Project. Pages 291–312 in R. O. Bierregaard, C. Gascon, T. E. Lovejoy, and R. Mesquita, editors. *Lessons from Amazonia: The ecology and conservation of a fragmented forest*. Yale University Press, New Haven, Connecticut, USA.
- Foster, J. R., P. A. Townsend, and C. E. Zganjar. 2008. Spatial and temporal patterns of gap dominance by low-canopy lianas detected using EO-1 Hyperion and Landsat Thematic Mapper. *Remote Sensing and Environment* 112:2104–2117.
- Fu, R., et al. 2013. Increased dry-season length over southern Amazonia in recent decades and its implication for future climate projection. *Proceedings of the National Academy of Sciences USA* 110:18110–18115.
- Granados, J., and C. Körner. 2002. In deep shade, elevated CO₂ increases the vigor of tropical climbing plants. *Global Change Biology* 8:1109–1117.
- Hättenschwiler, S., and C. Körner. 2003. Does elevated CO₂ facilitate naturalization of the non-indigenous *Prunus laurocerasus* in Swiss temperate forests? *Functional Ecology* 17:778–785.
- Huntingford, C., et al. 2013. Simulated resilience of tropical rainforests to CO₂-induced climate change. *Nature Geoscience* 6:268–273.
- Ingwell, L. L., S. J. Wright, K. K. Becklund, S. P. Hubbell, and S. A. Schnitzer. 2010. The impact of lianas on 10 years of tree growth and mortality on Barro Colorado Island, Panama. *Journal of Ecology* 98:879–887.
- Kato, R., Y. Tadaki, and H. Ogawa. 1978. Plant biomass and growth increment studies in Pasoh Forest. *Malaysian Nature Journal* 30:211–224.
- Körner, C. 2004. Through enhanced tree dynamics carbon enrichment may cause tropical forests to lose carbon. *Philosophical Transactions of the Royal Society of London B* 359:493–498.
- Körner, C. 2009. Responses of humid tropical trees to rising CO₂. *Annual Review of Ecology, Evolution, and Systematics* 40:61–79.
- Kurzel, B. P., S. A. Schnitzer, and W. P. Carson. 2006. Predicting liana crown location from stem diameter in three Panamanian lowland forests. *Biotropica* 38:262–266.
- Laurance, S. G., W. F. Laurance, A. Andrade, P. M. Fearnside, K. E. Harms, and R. C. C. Luizão. 2010. Influence of soils and topography on Amazonian tree diversity: A landscape-scale study. *Journal of Vegetation Science* 21:96–106.
- Laurance, S. G., W. F. Laurance, H. Nascimento, A. Andrade, P. M. Fearnside, E. Rebello, and R. Condit. 2009. Long-term variation in Amazon forest dynamics. *Journal of Vegetation Science* 20:323–333.
- Laurance, W. F. 2001. The hyper-diverse flora of the central Amazon: an overview. Pages 47–53 in R. O. Bierregaard, C. Gascon, T. E. Lovejoy, and R. Mesquita, editors. *Lessons from Amazonia: Ecology and conservation of a fragmented forest*. Yale University Press, New Haven, Connecticut, USA.
- Laurance, W. F., et al. 2011. The fate of Amazonian forest fragments: A 32-year investigation. *Biological Conservation* 144:56–67.
- Laurance, W. F., P. Delamonica, S. G. Laurance, H. L. Vasconcelos, and T. E. Lovejoy. 2000. Rainforest fragmentation kills big trees. *Nature* 404:836.
- Laurance, W. F., P. M. Fearnside, S. G. Laurance, P. Delamonica, T. E. Lovejoy, J. M. Rankin-de Merona, J. Q. Chambers, and C. Gascon. 1999. Relationship between soils and Amazon forest biomass: a landscape-scale study. *Forest Ecology and Management* 118:127–138.
- Laurance, W. F., L. V. Ferreira, J. M. Rankin-de Merona, and S. G. Laurance. 1998. Rain forest fragmentation and the dynamics of Amazonian tree communities. *Ecology* 79:2032–2040.
- Laurance, W. F., S. G. Laurance, L. V. Ferreira, J. M. Rankin-de Merona, C. Gascon, and T. E. Lovejoy. 1997. Biomass

- collapse in Amazonian forest fragments. *Science* 278:1117–1118.
- Laurance, W. F., T. E. Lovejoy, H. L. Vasconcelos, E. Bruna, R. K. Didham, P. C. Stouffer, C. Gascon, R. O. Bierregaard, S. G. Laurance, and E. Sampaio. 2002. Ecosystem decay of Amazonian forest fragments: A 22-year investigation. *Conservation Biology* 16:605–618.
- Laurance, W. F., H. Nascimento, S. G. Laurance, A. Andrade, P. M. Fearnside, and J. Ribeiro. 2006a. Rain forest fragmentation and the proliferation of successional trees. *Ecology* 87:469–482.
- Laurance, W. F., H. Nascimento, S. G. Laurance, A. Andrade, J. Ribeiro, J. P. Giraldo, T. Lovejoy, R. Condit, J. Chave, and S. D'Angelo. 2006b. Rapid decay of tree-community composition in Amazonian forest fragments. *Proceedings of the National Academy of Sciences USA* 103:19010–19014.
- Laurance, W. F., A. A. Oliveira, S. G. Laurance, R. Condit, C. Dick, A. Andrade, H. Nascimento, T. Lovejoy, and J. Ribeiro. 2005. Altered tree communities in undisturbed Amazonian forests: A consequence of global change? *Biotropica* 37:160–162.
- Laurance, W. F., A. A. Oliveira, S. G. Laurance, R. Condit, H. Nascimento, A. C. Sanchez-Thorin, T. E. Lovejoy, A. Andrade, S. D'Angelo, and C. Dick. 2004. Pervasive alteration of tree communities in undisturbed Amazonian forests. *Nature* 428:171–175.
- Laurance, W. F., D. Perez-Salicrup, P. Delamonica, P. M. Fearnside, S. D'Angelo, A. Jerzolimski, L. Pohl, and T. E. Lovejoy. 2001. Rain forest fragmentation and the structure of Amazonian liana communities. *Ecology* 82:105–116.
- Lewis, S. L., P. Brando, O. L. Phillips, G. van der Heijden, and D. Nepstad. 2011. The 2010 Amazon drought. *Science* 331:554.
- Lewis, S. L., Y. Malhi, and O. L. Phillips. 2004a. Fingerprinting the impacts of global change on tropical forests. *Philosophical Transactions of the Royal Society of London B* 359:437–462.
- Lewis, S. L., et al. 2004b. Tropical forest tree mortality, recruitment and turnover rates: Calculation, interpretation and comparison when census intervals vary. *Journal of Ecology* 92:929–944.
- Lovejoy, T. E., et al. 1986. Edge and other effects of isolation on Amazon forest fragments. Pages 257–285 in M. E. Soule, editor. *Conservation biology: The science of scarcity and diversity*. Sinauer, Sunderland, Massachusetts, USA.
- Mohan, J. E., L. H. Ziska, W. H. Schlesinger, R. B. Thomas, R. C. Sicher, K. George, and J. S. Clark. 2006. Biomass and toxicity responses of poison ivy (*Toxicodendron radicans*) to elevated atmospheric CO₂. *Proceedings of the National Academy of Sciences USA* 103:9086–9089.
- Phillips, O. L., and A. H. Gentry. 1994. Increasing turnover through time in tropical forests. *Science* 263:954–958.
- Phillips, O. L., et al. 2002. Increasing dominance of large lianas in Amazonian forests. *Nature* 418:770–774.
- Putz, F. E. 1983. Liana biomass and leaf area of a “tierra firme” forest in the Rio Negro Basin, Venezuela. *Biotropica* 15:185–189.
- Putz, F. E. 1984. The natural history of lianas on Barro Colorado Island, Panama. *Ecology* 65:1713–1724.
- Schnitzer, S. A. 2005. A mechanistic explanation for global patterns of liana abundance and distribution. *American Naturalist* 166:262–276.
- Schnitzer, S. A., and F. Bongers. 2002. The ecology of lianas and their role in forests. *Trends in Ecology and Evolution* 17:223–230.
- Schnitzer, S. A., and F. Bongers. 2011. Increasing liana abundance and biomass in tropical forests: Emerging patterns and putative mechanism. *Ecology Letters* 14:397–406.
- Schnitzer, S. A., and W. P. Carson. 2001. Treefall gaps and the maintenance of species diversity in a tropical forest. *Ecology* 82:913–919.
- Schnitzer, S. A., and W. P. Carson. 2010. Lianas suppress tree regeneration and diversity in treefall gaps. *Ecology Letters* 2010:849–857.
- Schnitzer, S. A., J. W. Dalling, and W. P. Carson. 2000. The impact of lianas on tree regeneration in tropical forest canopy gaps: Evidence for an alternative pathway of gap-phase regeneration. *Journal of Ecology* 88:655–666.
- Schnitzer, S. A., S. J. DeWalt, and J. Chave. 2006. Censusing and measuring lianas: A quantitative comparison of the common methods. *Biotropica* 38:581–591.
- Schnitzer, S. A., et al. 2012. Liana abundance, diversity, and distribution on Barro Colorado Island, Panama. *PLoS ONE* 7:e52114.
- Sheil, D., D. Burslem, and D. Alder. 1995. The interpretation and misinterpretation of mortality rate measures. *Journal of Ecology* 83:331–333.
- Stevens, G. C. 1987. Lianas as structural parasites: The *Bursera simaruba* example. *Ecology* 68:77–81.
- Webb, L. J. 1958. Cyclones as an ecological factor in tropical lowland rain forest, North Queensland. *Australian Journal of Botany* 6:220–228.
- Wright, S. J., O. Calderon, A. Hernandez, and S. Paton. 2004. Are lianas increasing in importance in tropical forests? A 17-year record from Panama. *Ecology* 85:484–489.
- Würth, M. K. R., K. Winter, and C. Körner. 1998. *In situ* responses to elevated CO₂ of tropical forest understory plants. *Functional Ecology* 12:886–895.
- Yorke, S. R., S. A. Schnitzer, J. Mascaro, S. G. Letcher, and W. P. Carson. 2013. Increasing liana abundance and basal area in a tropical forest: The contribution of long-distance clonal colonization. *Biotropica* 45:317–324.
- Zhu, S.-D., and K.-F. Cao. 2010. Contrasting cost-benefit strategy between lianas and trees in a tropical seasonal rain forest in southwestern China. *Oecologia* 163:591–599.
- Zotz, G., N. Cueni, and C. Körner. 2006. *In situ* growth stimulation of a temperate zone liana (*Hedera helix*) in elevated CO₂. *Functional Ecology* 20:763–769.
- Zuur, A. F., E. Ieno, N. Walker, A. Saveliev, and G. M. Smith. 2009. *Mixed effects models and extensions in ecology with R*. Springer, New York, New York, USA.