Liana effects on biomass dynamics strengthen during secondary forest succession

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Abstract. Secondary forests are important carbon sinks, but their biomass dynamics vary markedly within and across landscapes. The biotic and abiotic drivers of this variation are still not well understood. We tested the effects of soil resource availability and competition by lianas on the biomass dynamics of young secondary tropical forests in Panama and assessed the extent to which liana effects were mediated by soil resource availability. Over a five-year period, growth, mortality, and recruitment of woody plants of ≥1 cm diameter were monitored in 84 plots in 3–30-year-old secondary forests across the Agua Salud site in central Panama. Biomass dynamics and the effects of lianas and soil resources were examined using (generalized) linear mixed-effect models and a model averaging approach. There was strong spatial and temporal variation in liana biomass within and across the plots. The relative biomass of lianas had a strong negative effect on overall tree growth, growth of understory trees decreased with soil fertility and dry season soil water content, and the effect of lianas on tree mortality varied with soil fertility. Tree recruitment was not associated with any of the predictor variables. Our model indicates that tree biomass growth across our landscape was reduced with 22% due to competition with lianas, and that the effect of lianas increased during succession, from 19% after five years to 32% after 30 years. The projected liana-induced growth reduction after 60 years was 47%, which was consistent with data from a nearby site. Our study shows that the observed liana proliferation across tropical forests may reduce the sequestration and storage of carbon in young secondary forests, with important implications for the carbon balance of tropical forest landscapes and consequently for global climate change. Our study highlights the need to incorporate lianas and soil variables in research on the biomass dynamics of secondary forest across tropical landscapes, and the need for well-replicated longitudinal studies to cover landscape-level variability in the relevant abiotic and biotic components.

Key words: biomass; competition; growth; lianas; mortality; Panama; recruitment; secondary forests; soil nutrients; succession.

Introduction

More than one-half of the world's tropical forests are naturally regenerating secondary forests on logged or post-agricultural lands (FAO 2010), which represent a huge carbon sequestration potential (Yang et al. 2010, Pan et al. 2011, Chazdon et al. 2016, Poorter et al. 2016). Accurate predictions of the biomass dynamics of these forests are critical to understand their role in mitigating climate change, to improve global climate change models (Grace et al. 2014, Chazdon et al. 2016, Verbeeck and Kearsley 2016), and to support intergovernmental and national discussions on climate-change related policies (Agrawal et al. 2011). Yet there is considerable uncertainty in the biomass dynamics of successional forests (Norden et al. 2015). This uncertainty has been attributed to variation in previous land use, local biotic and abiotic

conditions as well as to stochasticity and historical contingency (van Breugel et al. 2012, Arroyo-Rodríguez et al. 2014, Jakovac et al. 2015, Norden et al. 2015). Despite this uncertainty, field tests that examine how biotic (e.g., competition by non-tree growth forms) and abiotic factors (e.g., soil resources) influence secondary forest biomass dynamics remain scarce (Duncan and Chapman 2003, Davidson et al. 2004, Siddique et al. 2009, van der Heijden et al. 2015).

Although canopy trees are the major component of forests in terms of biomass, other growth forms such as lianas can be abundant and play an important role in forest dynamics (Schnitzer and Bongers 2002). Tobin et al. (2012) pointed out that, for the same biomass, lianas can have a larger competitive impact on trees than competing trees. Lianas seem to be increasing in abundance and biomass across the tropics and can have strong effects on the biomass dynamics of forests (Phillips et al. 2002, Schnitzer and Bongers 2011, van der Heijden et al. 2015) by reducing the growth and survival of individual host trees through competition for light and soil resources

(Schnitzer et al. 2005, Toledo-Aceves and Swaine 2008, Wright et al. 2015), or causing physical damage by mechanical loading or collateral tree fall (Putz and Appanah 1984, Vidal et al. 1997, Schnitzer and Bongers 2011). At the stand level, high densities of lianas can arrest tropical forest succession (Tymen et al. 2016) or inhibit the recovery of biomass and diversity of trees in gaps and during the mid-successional phase (Clark and Clark 1990, Ingwell et al. 2010, Schnitzer and Carson 2010). Although lianas can become abundant in secondary forests (Dewalt et al. 2000, Letcher and Chazdon 2009*b*, Barry et al. 2015), how they affect the first decades of successional forest dynamics remains an open question.

Lianas compete strongly for light with larger canopy trees (van der Heijden et al. 2015), regeneration in canopy gaps (Schnitzer and Carson 2010), or seedlings growing under open canopy conditions (Schnitzer et al. 2005). However, plants in the understory of early successional forests are already strongly limited by the asymmetric competition for light from neighboring canopy trees (Lewis and Tanner 2000, van Breugel et al. 2006, 2012). When lianas are present in a forest canopy, they replace, rather than add to the leaf biomass of trees in a secondary forest canopy (Rodríguez-Ronderos et al. 2016) and might therefore have little impact on light levels below the main canopy. Indeed, Toledo-Aceves and Swaine (2008) found that lianas reduced the biomass of saplings of two tree species in large gaps, but not in smaller gaps or forest understory. Thus, the response of the smallest trees to lianas might differ from that of the largest trees in a secondary forest community.

Controlled experiments have demonstrated that lianas not only compete with seedlings, saplings and adult trees for light, but also for soil resources (see overview in Toledo-Aceves 2014). Effects of lianas on trees will be driven by spatial or temporal heterogeneity in soil nutrients and water when (1) these resources are limiting and (2) when lianas and trees differ in traits and tradeoffs related to survival and the capture, use and conservation of these resources. For example, in a seasonal forest in central Panama, effects of liana cutting on transpiration of trees varied with seasonal changes in soil moisture (Tobin et al. 2012, Álvarez-Cansino et al. 2015). Trait differences between lianas and trees have been found in a wide range of studies (Kazda and Salzer 2000, Cai et al. 2009, Zhu and Cao 2010, Asner and Martin 2012, van der Sande et al. 2013, Wyka et al. 2013, Chen et al. 2015, 2016, De Guzman et al. 2016). However, these studies have led to contrasting conclusions about the strength of liana competition in relationship to soil resources. Some authors suggest that lianas capture resources more effectively, enabling them to compete stronger with trees when light availability and soil resources are abundant (e.g., Schnitzer and Bongers 2002, Asner and Martin 2012, Kazda 2015). In contrast, others hypothesize that a higher nutrient use efficiency or tolerance to resource scarcity enables lianas to compete more strongly when belowground resources are limited (e.g., Chen et al. 2015).

In this study, we used one of the largest landscape scale studies on secondary forest dynamics in the tropics, with 54 forest patches across the Agua Salud landscape in central Panama (van Breugel et al. 2013), to evaluate the effect of lianas on biomass dynamics during succession. Combining the points discussed above, we hypothesized that (1) lianas are associated with slower tree growth, higher mortality, and lower recruitment, (2) effects of lianas on tree growth, mortality, or recruitment vary along gradients of soil fertility and dry season soil water content, and (3) lianas have a stronger impact on the growth and mortality of the larger trees than on the smallest trees of young secondary forest communities.

METHODS

Study area and vegetation censuses

The 15-km^2 Agua Salud study area is situated in the central part of the Panama Canal Watershed. The area receives 2700 mm of annual rainfall and has a dry season from mid-December to early May (Ogden et al. 2013). Soils are strongly weathered, infertile, and well-drained Oxisols with little variation in topsoil texture (silty clays to clays) and soil nutrient concentrations (Appendix S1: Table S1). The landscape consists of a mosaic of cattle pastures and cultivated fields, fallows, secondary forests, and fragments of older secondary forest.

We used data from 84 plots at 42 secondary forest sites (Appendix S1) that were selected at random and represent an unbiased, representative sample of landscape-wide variation in age, structure, and composition (van Breugel et al. 2013). Time since abandonment of the sites varied from 3 to 32 years, with a fairly even distribution along this range (Fig. 1). We monitored growth, mortality, and recruitment of woody plants from 2009 until 2014. In each plot, all stems of trees and shrubs with a diameter at breast height (dbh) ≥5 cm and lianas stems with a diameter ≥1 cm were identified to species, labeled, and their dbh was measured. In one-half of each plot, all tree and shrub stems ≥1 cm dbh were treated similarly. See Appendix S1 for more details on study area and vegetation censuses.

Stand dynamics

We calculated the aboveground biomass (AGB, kg/m^2) of trees using locally developed allometric equations (van Breugel et al. 2011) and liana AGB using an allometric equation developed by Schnitzer et al. (2006; Appendix S1). Stand-level AGB growth rate (kg·m^{-2}·yr^{-1}, henceforth "growth") was calculated as the AGB gains from growth of trees recorded in 2009 that survived until 2014 (surv) divided by the period between the 2009 and the 2014 censuses in years (Δt), plus AGB gains from trees recruited since 2010 divided by Δt (recr): growth = $(AGB_{surv,2014} - AGB_{surv,2009}/\Delta t) + (AGB_{recr,2014}/\Delta t)$. Recruitment was calculated as the proportion of trees in the
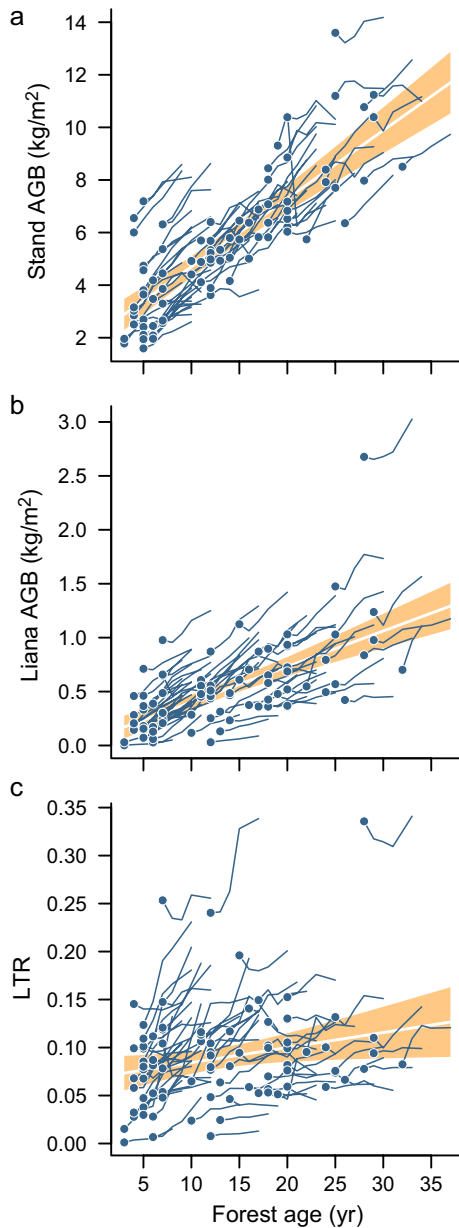
Fig. 1. Successional trajectories of (a) stand-level aboveground biomass (AGB), (b) liana AGB, and (c) liana:tree ratio (LTR) across forest age. White lines and shaded areas are the best fit regression splines with 95% CI. Dark dots and lines are plot values in 2009, followed by changes from 2009 to 2014, respectively. [Colour figure can be viewed at wileyonlinelibrary. com]

quadrants with 1 cm dbh limit that were recorded in 2014 but not in 2009, while mortality was calculated as the proportion of trees from the 2009 census that were dead in 2014.

We calculated the stand-level growth and mortality for all trees combined, as well as for two different size classes: "large trees" and "small trees." Large trees included the trees in the top 25th percentile in terms of dbh of each

plot and small trees included the trees in the bottom 25th percentile.

Explanatory variables

The explanatory variables included initial stand-level AGB in 2009 (excluding lianas, AGB_i, kg/m^2) and AGB_{lianas}/AGB_{trees} (liana:tree ratio, hereafter LTR). There was large among-plot variation in rates of change in LTR with very rapid increases in LTR in many of the youngest and some of the older plots (Fig. 1). The initial LTR would underestimate the effect of lianas in these plots. Therefore, we used the mean LTR over 2009–2014 as an explanatory variable. In addition, we used the dry-season soil water content (SWC; Appendix S1) and the scores on the first two axes of a principal component analysis of 10 soil nutrient variables (S1 and S2, respectively; Appendix S1: Fig. S2) as explanatory variables.

Statistical analyses

We modelled changes in stand-level AGB, liana AGB, and LTR as a function of forest age using generalized additive mixed models (GAMMs) with thin plate regression spline smoothing to allow for non-linearity (Wood 2006), if any, and plots within sites as random effect in order to account for the hierarchical sampling design.

Stand-level growth, mortality, and recruitment were each modelled as a function of LTR, AGB_i, S1, S2, and SWC. We used a model averaging approach with a "global model" that only included interactions between LTR and the other explanatory variables: $Y \sim LTR \times (AGB_i + S1 + S2 + SWC)$. In all analyses, both AGB_i and LTR were square-root transformed to improve the homogeneity of residual variance. All explanatory variables were standardized to a mean of zero and a standard deviation of 0.5 prior to analyses (Grueber et al. 2011).

Stand-level growth was modelled in linear mixed effect models (LMEs) with plots within site as random effect. Heteroscedasticity in the residuals was found to be primarily caused by AGB_i. We used an exponential variance structure to account for this as it led to the greatest reduction in the Akaike information criterion adjusted for sample size (AIC$_c$; Pinheiro and Bates 2004, Zuur et al. 2009). Because mortality and recruitment are proportional variables, they were modelled using generalized linear mixed-effects models (GLMMs) with binomial family and logit link function (Bolker et al. 2009). Each global model was dredged to generate a list of candidate models that were ranked by AIC$_c$ (for growth) or quasi-AIC$_c$ (QAIC$_c$; for mortality and recruitment, because GLMMs had overdispersion; Burnham and Anderson 2002). Model averaging was performed using candidate models within the top 2 AIC$_c$ or QAIC$_c$ units (Burnham and Anderson 2002), using a full-averaging approach (Appendix S1). We calculated the mean ± SE of the marginal and conditional R^2_{GLMM} of all selected candidate models and the "variable importance" for each

variable. The former represent the variance explained by the fixed effects and fixed + random effects, respectively, and the latter can be interpreted as the probability that a variable is a component of the best model (Appendix S1).

We used the final averaged model for growth of "all trees" to predict forest-level tree biomass growth (1) with LTR at observed values ($G_{t,\text{LTR}=\text{ov}}$) and (2) with LTR set at zero ($G_{t,\text{LTR}=0}$). In both cases, all other stand variables were set at their observed values. Liana-induced loss in tree biomass growth ($G_{t,\text{loss}}$) was calculated as 100 × (predicted $G_{t,\text{LTR}=0} - G_{t,\text{LTR}=\text{ov}}$)/$G_{t,\text{LTR}=0}$. Compensation of $G_{t,\text{loss}}$ by the biomass growth of liana themselves (G_l) was calculated as 100 × $G_l/G_{t,\text{loss}}$. We analyzed both response variables as a function of forest age in linear mixed effects models, with plot within sites as random effects. Percentage compensation of liana was log-transformed during analysis.

All statistical analyses were performed in R v3.2.4 (R Core Team 2016). Principle component analysis for soil nutrients were conducted with the prcomp function (Becker et al. 1988), GAMMs with the mgcv package (Wood 2006), LMEs with the nlme package (Pinheiro and Bates 2004), and GLMMs with the lme4 package (Bates et al. 2015). Model dredging, model averaging, variable importance, and R^2_{GLMM} was implemented with the MuMIn package (Bartoń 2013).

RESULTS

General patterns

Overall, stand AGB and biomass of lianas increased with forest age. As has been noted elsewhere (van Breugel et al. 2006, Norden et al. 2015), short-term successional dynamics were highly variable across sites (Fig. 1). Initial values of LTR and changes in LTR differed strongly among plots, with dramatic increases in LTR in many of the youngest plots and some of the older plots (Fig. 1b, c).

The averaged models explained 37–51% of the variation in stand growth and 5–13% of the variation in mortality and recruitment. AGB_i was selected in all (growth and mortality) or most (recruitment) models, but the variable importance of LTR and soil variables differed considerably across the average models (0.08–1.00; Appendix S2: Table S1).

Liana effects and liana–soil interactions

LTR had a strong negative effect on the growth of all trees combined (Fig. 2; Appendix S3: Fig. S1). The final averaged models for small and large trees included an LTR effect with a larger LTR effect (slope) in the "large tree" model. However, in both models, evidence of an LTR effect was weak, as the confidence interval of the effect sizes overlapped with zero (Fig. 2; Appendix S2: Table S1). The effect of lianas on the mortality of small trees varied with soil fertility (LTR × S1 effect; Fig. 2). While LTR had a negative impact on tree survival on more fertile soils, on soils with lower nutrient concentrations survival of smaller trees was positively associated with LTR (Appendix S3: Fig. S2). There was no support for any other LTR interaction effect (Fig. 2).

Across the landscape, the predicted mean stand-level tree growth without lianas (LTR = 0) was 1.28 times higher than the predicted growth with lianas (LTR set at
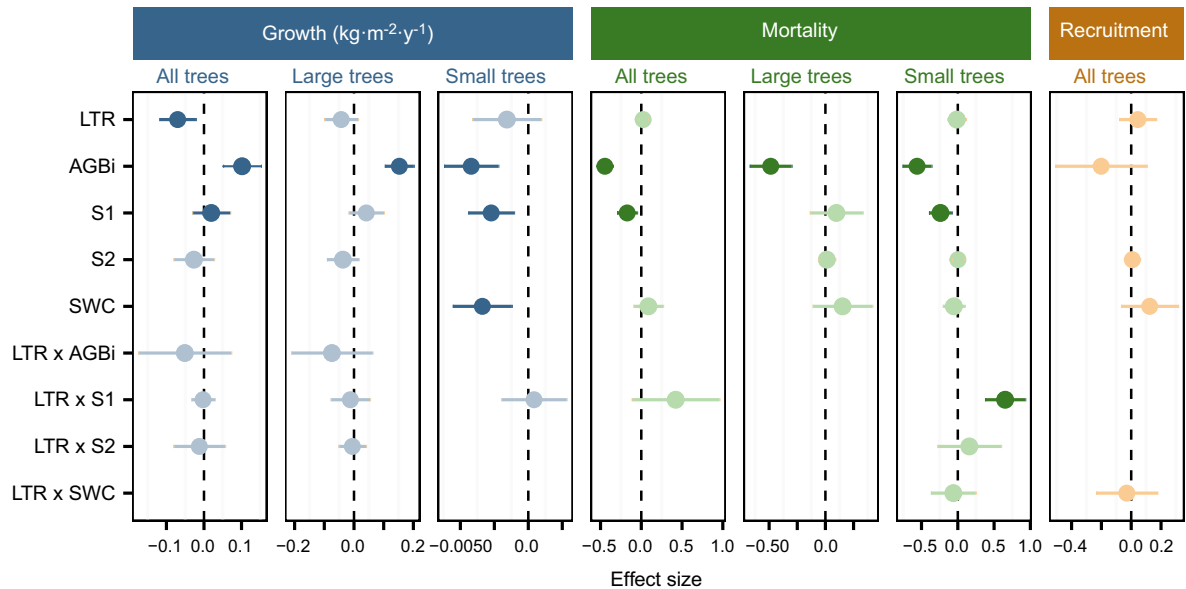

FIG. 2. Coefficient plots from the averaged liana models. Response variables are indicated above the graphs. Points are averaged coefficient estimates and bars are corresponding 95% CIs. Darker colored circles and bars denote effect sizes that do not overlap with zero, while brighter circles and bars denote effect sizes that overlap with zero. Confidence intervals that do not overlap with zero value denote strong and large effects. LTR, liana:tree ratio; AGB_i, initial stand AGB; S1, soil PC1 axis; S2, soil PC2 axis; SWC, soil water content. [Colour figure can be viewed at wileyonlinelibrary.com]
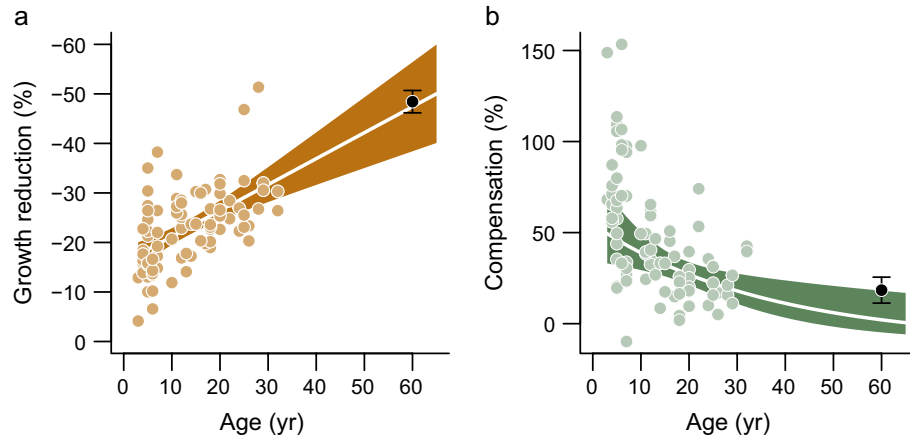
Fig. 3. Effect of lianas on biomass dynamics of secondary forests along a successional gradient. (a) Liana-induced loss in tree biomass growth. (b) Compensation of this loss by the biomass growth of lianas themselves. Colored dots are Agua Salud plots; white lines and shaded areas are fitted regression lines ± 95% CI. We extrapolated our regression models to 65 yr to compare the predictions of our models with observed values from a liana-removal experiment in a nearby 60-yr-old secondary forest (black dots with 95% CI bars; data from van der Heijden et al. 2015; see Appendix S5 for details). [Colour figure can be viewed at wileyonlinelibrary.com]

observed values; 0.55 ± 0.04 vs. 0.43 ± 0.01 kg·m^{-2}·yr^{-1}, mean ± CI). Effect of lianas on tree biomass growth varied with successional age of the forest, with predicted tree growth reduction increasing from 19% after five years to 32% after thirty years (Fig. 3a). Liana biomass growth compensated 56% of the predicted loss in tree biomass growth in five-year-old forests and this decreased to 28% in 30-year-old forests (Fig. 3b).

Other main effects (soil and AGBi)

Biomass growth of the large trees and of all trees combined was positively related to AGB$_i$ but only very weakly to S1 and not to SWC. Small tree growth was negatively associated with AGB$_i$, S1, and SWC (Fig. 2). The negative effects of the soil variables may reflect a positive effect on the growth of the larger trees, and thus stronger asymmetric competition with their smaller neighbors (van Breugel et al. 2006, 2012), rather than a direct negative effect of higher soil fertility or of dry season soil water content.

Discussion

There was strong spatial and temporal variation in liana biomass within and across the early secondary forests in the Agua Salud landscape, both in absolute terms and relative to total stand biomass. This variation in liana biomass accounted for part of the variation in biomass dynamics across these secondary forests. An important result from this study is the prediction that the effect of lianas on tree biomass growth strengthens during succession (Fig. 3). Our final averaged model provided partial support for the hypothesis that lianas affect tree performance: lianas reduced stand-level tree biomass growth and affected the mortality of the smallest trees, but tree recruitment was not

associated with relative liana biomass. The effect of lianas on tree mortality varied with soil fertility, providing some support for the hypothesis that liana effects vary along gradients of soil resource availability. Our data showed only weak evidence for a stronger liana effect on canopy trees than on the understory trees (growth) and the opposite pattern in the case of small tree mortality.

Effects of lianas on tree growth

Several recent studies, many of them from Barro Colorado Nature Monument (BCNM) located at about 12 km from our site, have shown that high densities of lianas inhibit tree regeneration, cause tree mortality, and reduce tree growth and carbon accumulation in old secondary and mature tropical forests (Ingwell et al. 2010, Schnitzer and Carson 2010, Tobin et al. 2012, Duran and Gianoli 2013, van der Heijden et al. 2015, Wright et al. 2015, Tymen et al. 2016). The present study is, to our knowledge, the first to examine the effects of lianas on biomass dynamics during the first few decades of young tropical forest succession.

As found in older forests, lianas had a substantial impact on tree biomass growth. Across our landscape, lianas reduced total tree biomass growth by 22%. Interestingly, the predicted negative effect of lianas on tree growth increased significantly during succession, from 19% after five years to 32% after 30 years and 47% after 60 years. The latter was surprisingly similar to the observed reduction in tree growth in a liana removal experiment in a 60-year-old secondary forest in BCNM (48% ± 2%; Fig. 3a; van der Heijden et al. 2015). Biomass gain by growth of lianas themselves compensated >50% of the predicted liana-induced loss in tree biomass growth early in succession, but compensated much less of the loss in tree growth in older forests (Fig. 3b). This reflects that

lianas rely on trees for support, invest less in carbon-dense stems, and therefore contribute relatively little to total stand biomass (Laurance et al. 1997, van der Heijden et al. 2013, 2015, Wright et al. 2015).

Lianas compete directly with canopy trees for light. However, understory trees are strongly limited by the asymmetric competition for light by the tree canopy (van Breugel et al. 2012). Only when lianas would draw light levels to even lower levels, we would expect lianas to affect growth of understory trees, yet we did not find a significant liana effect on understory light availability in our plots (Appendix S4). This concurs with findings of Rodríguez-Ronderos et al. (2016) who found that within four years after liana removal in a 60-year-old secondary forest, trees had fully compensated for the loss of liana leaf biomass in the canopy. In other words, when present in a forest canopy, lianas substitute for, rather than add to, tree leaf biomass. Indeed, we found that the effect size of lianas on the growth of the small trees was close to zero (−0.002). The effect size of lianas on the growth of the larger trees in our plots was much stronger (−0.043), even though its 95% CI just overlapped with zero (Fig. 2; Appendix S2: Table S1).

Effects of lianas on tree mortality and recruitment

We found no effect of lianas on the mortality of large trees in our 3–30-year-old forests (Fig. 2). This may have been partially due to the large variation in mortality among plots. While resource competition will directly limit growth, its effect on tree mortality might be less direct or more delayed. Mortality can also be driven by diseases or other factors that may or may not be directly related to or driven by competition (Lewis and Tanner 2000, van Breugel et al. 2006). Lianas had a negative effect on the survival of the smaller understory trees on more fertile soils but a positive effect on poorer soils (Appendix S3: Fig. S2). Especially the latter pattern is difficult to interpret or explain. None of the variables in our model explained recruitment. Recruitment was very variable across plots and might have been more related to dispersal and landscape factors (Nathan and Muller-Landau 2000, Chazdon et al. 2007), rather than with the local site variables that were included in our analysis.

Liana–soil interactions

We hypothesized that the impact of lianas on trees is mediated by variation in soil resource availability when co-occurring lianas and trees differ in traits and trade-offs related to the capture, use, and conservation of nutrients and water, and when soil nutrients or water are limiting. Lianas and trees have been found to differ in key traits at several tropical forest sites (e.g., Cai et al. 2009, van der Sande et al. 2013, De Guzman et al. 2016). In addition, our research site has a distinct dry season (Ogden et al. 2013) and the soils in our study area have relatively low concentrations of plant-available P and exchangeable base cations compared to forests in the region and the wider tropics (Appendix S1: Table S1; Quesada et al. 2010, Condit et al. 2013). At low nutrient concentrations, small changes may have disproportionally large effects on tree growth and plant species' competitive hierarchy (Tilman 1985, Vitousek and Sanford 1986, Wright et al. 2011, Santiago et al. 2012, Condit et al. 2013). Nonetheless, our data provided little evidence that liana effects on forest-level tree biomass dynamics are mediated by soil resources. This suggests that, on community level, other factors outweigh these liana × soil interaction effects, or that trait differences between lianas and trees are not consistent across the dominant species in our forests.

Uncertainties in successional dynamics

Recent studies on biomass dynamics of secondary forests have shown that the successional dynamics of individual sites are to a large extent unpredictable (Arroyo-Rodriguez et al. 2015, Norden et al. 2015). Attempts to predict successional trajectories have been limited to statistical models that predict biomass dynamics as a function of stand age and initial stand structure, and in a few cases diversity and functional composition (Lohbeck et al. 2013, 2015, Norden et al. 2015). Our results showed that lianas can contribute to the heterogeneity in successional dynamics across secondary tropical forest sites, but field studies on their impacts on secondary forest dynamics are very rare (Letcher and Chazdon 2009b, Schnitzer et al. 2016). Similarly, spatial heterogeneity in soil fertility may play a role. Although this role has long been recognized (Uhl 1987, Buschbacher et al. 1988, Finegan 1996, Guariguata and Ostertag 2001, Chazdon et al. 2007, Siddique et al. 2009), few secondary forest dynamics studies include soil data. Our work highlights the need for highly replicated studies that cover landscape-level variability in liana densities and soil variables to advance the ongoing discussion on the stochastic vs. deterministic nature of secondary forests succession (Gleason 1927, Clements 1936, Arroyo-Rodriguez et al. 2015, Norden et al. 2015).

Implications of liana–tree interactions

Liana removal is sometimes advocated to promote forest regeneration (Perez-Salicrup et al. 2001, Grauel and Putz 2004, Addo-Fordjour et al. 2013). Our data suggests that this would indeed aid in accelerating successional biomass growth in secondary forests with substantial liana biomass. However, lianas provide ecosystem functions that play important roles in secondary forest succession. They might, for example, accelerate leaf cover build up and canopy closure, limit soil erosion and nutrient leaching, and distribute nutrients more efficiently through litter fall (Powers 2014, Campbell et al. 2015, Kazda 2015). Lianas also provide food, shelter, and habitat connectivity for wildlife (Gentry 1992, Yanoviak and Schnitzer 2013, Arroyo-Rodríguez et al. 2014, Michel et al. 2014, Yanoviak 2014), thus indirectly aiding tree

seed dispersal. Plans to include liana cutting as part of forest restoration or forest management strategies should thus consider the interactions and functions of lianas beyond their direct competition effects on the biomass dynamics of the tree community.

Recent studies by Poorter et al. (2016) and Chazdon et al. (2016) have highlighted the potential of secondary forest to sequester large amounts of carbon and partially counterbalance carbon emissions from deforestation and other sources of CO_2 emissions. Lianas are common in early successional forests (Letcher and Chazdon 2009*a*, Barry et al. 2015) and can be expected to become increasingly abundant with increasing land-use intensity and decreasing fallow periods (Schnitzer and Bongers 2011, Jakovac et al. 2015, Tymen et al. 2016). Here we have shown that (1) the proliferation of lianas can have large negative impacts on the sequestration and storage of carbon in secondary forests across human-modified landscapes and (2) this impact strengthen with successional age of secondary forests (van der Heijden et al. 2015, this study). The incorporation of lianas in global vegetation models may thus be critical to improving these models and for predicting changes in the future carbon dynamics of tropical forest landscapes (Verbeeck and Kearsley 2016). However, most research on the role of lianas in forest ecosystems is geographically restricted and, as a consequence, there is little data on how the strength of liana competition varies across biogeographical regions and along environmental gradients such as precipitation (DeWalt et al. 2010, Schnitzer and Bongers 2011). We agree with Schnitzer et al. (2016) that experiments and observational studies on the effects of lianas need to be replicated across tropical forest types and regions to accurately parameterize global vegetation models. We add that, given the increasingly important role of tropical forest regrowth in the global carbon cycle and in restoring vital ecosystem services, we need to set up experimental or highly replicated longitudinal studies on the effects of lianas across successional gradients.

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Supporting Information