COMMUNITY ECOLOGY – ORIGINAL RESEARCH

Lianas do not reduce tree biomass accumulation in young successional tropical dry forests

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Abstract

Young successional tropical forests are crucial in the global carbon cycle because they can quickly sequester large quantities of atmospheric carbon. However, lianas (woody vines) can significantly decrease biomass accumulation in young regenerating forests. Lianas are abundant in tropical dry forests, and thus we hypothesized that lianas reduce biomass accretion in dry forests. Lianas may be particularly detrimental to the growth of young trees, which are vulnerable to competition from lianas. Alternatively, lianas may have a stronger negative effect on the largest trees because lianas seek the high-light environment at the top of the forest canopy. We tested these hypotheses using a liana-removal experiment in 13 dry forest stands that ranged from 1 to 70 years in southwestern Panama. We measured biomass accumulation annually for more than 10,000 stems from 2013 to 2017. Contrary to our expectations, liana removal had no effect on tree biomass accumulation across our successional forests and throughout our study period. Liana removal did not benefit smaller trees or larger trees. Lianas did not increase biomass accumulation on recruits, and did not increase biomass loss due to mortality. Surprisingly, removing lianas had a negative effect on three out of 41 tree species. Lianas had no effect on biomass accumulation and loss, possibly because: (1) trees allocated resources to roots instead of stems, (2) trees and lianas partitioned water, (3) higher irradiance after liana removal reduced soil moisture, or (4) low water availability might have been such a strong stressor that it reduced plant–plant competition.

Keywords Biomass accretion · Biomass loss · Forest regeneration · Removal experiment · Tree size

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Introduction

Deforestation of old-growth forests continues at unprecedented rates worldwide, particularly in the tropics (FAO 2015). However, the amount of area covered by secondary tropical forests is increasing rapidly and it now exceeds the area covered by old-growth forests (FAO 2015). The recent expansion of young secondary tropical forests has been dramatic; the area of regenerating forests in the neotropics increased by 66% between 1990 and 2007 (Aide et al. 2013). The rapid expansion of secondary forests is expected to partially compensate for the ecosystem services that are lost by the loss of old-growth forests, at least in terms of biomass accumulation and biomass storage (Baccini et al. 2012; Chazdon et al. 2016). Young tropical secondary forests are particularly important for the global carbon cycle because they rapidly accrue large amounts of biomass during the first four decades of forest regeneration (Poorter et al. 2016), as trees profit from the high-light conditions after farmland abandonment (van Breugel et al. 2012; Jakovac et al. 2014).

If left unperturbed, regenerating forests are expected to eventually compensate for the loss of carbon that was previously stored in old-growth forests (Chazdon et al. 2016; Poorter et al. 2016).

Recent studies, however, suggest that the potential for fast biomass accumulation of early secondary tropical forests may fail to compensate for the loss of carbon because of the effects of strong plant–plant interactions. One of the strongest plant–plant interactions in tropical forests takes place between trees and lianas (Estrada-Villegas and Schnitzer 2018), where lianas compete intensely with trees for both above and belowground resources (Toledo-Aceves 2015). In young secondary forests, lianas are particularly abundant (Dewalt et al. 2000; Letcher 2015; César et al. 2017), where they can disrupt the trajectory of biomass accumulation. For example, liana density in young forests (5-years-old) in Panama exceeded the density of lianas in nearby old-growth forests (Barry et al. 2015). In Côte d'Ivorie and Costa Rica, liana density in 20-year-old forests was 38–47% higher, respectively, compared to old-growth forests (Kuzee and Bongers 2005; Letcher and Chazdon 2009). Lianas may also disrupt the trajectory of biomass accumulation as forests age because the ratio of liana density relative to tree density increases sharply in the first 10 years after abandonment, decreasing the amount of biomass that trees accumulate (Lai et al. 2017).

Recent experimental evidence suggests that lianas significantly reduce biomass accumulation in secondary forests. For example, in a large liana-removal experiment in a 60-year-old secondary forest in central Panama, lianas reduced biomass production by 76% per year for 3 years (van der Heijden et al. 2015). In liana-removal experiments in treefall gaps, tree growth and tree biomass accumulation were 55–180% higher compared to control plots in intact forest (Schnitzer and Carson 2010; Schnitzer et al. 2014). In other liana-removal experiments, tree sapling biomass increased between 52 and 436% in liana-removal plots compared to control plots (Schnitzer et al. 2005; César et al. 2016). However, the reduction in biomass accumulation from liana competition is not homogeneous across the forest. For example, the relative effect of lianas on biomass accretion was greater on larger trees than on smaller trees in the same competitive environment (Lai et al. 2017; Estrada-Villegas et al. 2020). Combined, these findings indicate that the detrimental effect of lianas is stronger on large trees, which contribute the most to carbon storage. Furthermore, liana density and biomass have been increasing in tropical forests (Schnitzer and Bongers 2011; Schnitzer 2015), so their effect on forest biomass accumulation may also be increasing.

Most liana-removal studies have been conducted in tropical moist and wet forests, and there is a conspicuous lack of liana-removal manipulations in tropical dry forests and in forests that vary in age (Estrada-Villegas and Schnitzer 2018). For example, there have been 15 liana cutting experiments in moist or wet forests, but only six liana cutting experiments in dry forests, and these latter experiments were conducted at a limited spatial scale and with a small number of trees. Furthermore, only one previous study experimentally tested the effects of lianas across forests of different ages. Specifically, in a liana-removal experiment in an young secondary moist forest in Panama, Estrada-Villegas et al. (2020) found that lianas decreased relative biomass accumulation between 13 and 22% in forests that ranged from 10 to 35-years old. No study has explicitly evaluated the effects of lianas on forest biomass accumulation in tropical dry forests, and whether such effects mirror what has been found in moist forests. Moreover, it is unclear whether lianas reduce biomass accumulation in older secondary forests as strongly as they do in younger secondary forests (Lai et al. 2017; Estrada-Villegas et al. 2020).

In this study, we used a liana-removal experiment in 13 forest stands that varied in age to evaluate whether lianas reduced forest biomass accumulation in different aged tropical dry forests. The forest stands ranged from 3 to 70 years in age and were located at the tip of the Azuero peninsula, in the southwestern part of Panama. We hypothesized that lianas will have a strong negative effect on tree biomass accumulation because lianas compete intensely with co-occurring trees. We expected that trees with lianas in their crowns (in control plots) would accrue less biomass than trees without lianas (in liana-removal plots). Based on our previous findings (Estrada-Villegas et al. 2020), we hypothesized (H1) that lianas will reduce biomass due to both the reduction of tree growth and increase in tree mortality (Ingwell et al. 2010; van der Heijden et al. 2015). Our second hypothesis (H2) was that lianas would have the strongest negative effect on the largest trees, independent of forest age because lianas seek areas with high-light conditions found at the top of the largest trees. Alternatively, (H3) lianas will have the strongest effect on the small trees in the younger forests because lianas can easily smother the small trees that make up the incipient canopy. By contrast, in older forests, many larger trees are able to withstand lianas on their canopy (Visser et al. 2018).

Methods

Study site

In 2009, we established a chronosequence of secondary forests in the municipality of Pedasi, province of Los Santos, in Western Panama (7°25′30″N; 80°10′30″W). Large tracts of land in Pedasi were cleared by the 1960s for cattle ranching (Heckadom-Moreno 1984), but cattle production declined from 2000 to 2010, leading to land abandonment

and ~4% net forest gain in the region during that decade (Caughlin et al. 2016). The chronosequence is located in areas that were originally logged in the 1970s, underwent regular prescribed burnings for pasture management, and were abandoned in 1997, 1999, 2000 and 2008. An adjacent area has been forested since 1939 and thus represents a stand that was 70-years old when our inventories began. Dates of abandonment were confirmed with landowners and locals from the municipality, and none of the areas have been logged or burnt since they were abandoned.

The forests in Pedasi are classified as tropical dry (Holdridge 1964), with a mean annual precipitation of 1706 mm (data from 1976 to 2017 provided by Empresa de Transmisión Eléctrica S.A., Cañas Station). Annual precipitation during our study period (2013–2017) were 1557 mm, 1930 mm, 613 mm, 1114 mm, and 1369 mm. Our study area experienced an ENSO (El Niño and the Southern Oscillation) event in 2015, where rainfall was particularly low. The mean annual temperature is 25 °C, and the dry season is from December until May (Griscom et al. 2011). Detailed information about these areas can be found elsewhere (Griscom et al. 2009, 2011; Estrada-Villegas et al. 2019).

Sampling methods and data collection

The chronosequence comprised 13 forested stands, each with two plots (50×20 m), one upslope and another downslope. The stands ranged from 1 to 70 years-old when we established the plots in 2009. In 2012, we established a third plot per site for the liana-removal manipulation. In each plot, we tagged, measured, and identified to species all trees, shrubs and lianas ≥ 5 cm diameter at breast height (DBH, measured on marked locations on trees at 1.3 m from the ground, and on lianas at 1.3 m from the last rooting point). We also tagged, measured, and identified all trees, shrubs and lianas with a diameter ≥ 1 cm in one half of each plot (first and second column lengthwise, 5×50 m per column). Sampling methods followed van Breugel et al. (2013) and Schnitzer et al. (2008). Lianas were not measured in the manipulation plots. To assign a control plot per site, we calculated the total basal area and total stem density for all three plots using data from 2012, and then selected one of the two non-manipulated plots that was most similar to the manipulated plot.

In 2013, we cut all lianas in each removal plot and in a 5 m buffer around each removal plot. We also cut all lianas rooted outside of the buffer that were growing into the plot. Lianas were cut at ground level and at shoulder level to avoid re-sprouting. We did not dislodge lianas from trees to avoid damaging tree crowns (follows Schnitzer and Carson 2010). Once per year, we re-cut new sprouts produced by cut lianas, as well as any new lianas growing into the plots. We conducted annual censuses of all plots from 2013 to 2017. Across all plots, we measured a total of 10,581 stems

in 2013, and 9871 stems in 2017. We identified > 98% of individuals to species. The datasets generated during and/or analyzed in this study are available from the corresponding author on reasonable request.

Data analysis

To evaluate the effect of lianas on the changes in forest biomass across succession, we partitioned biomass in four sources: (1) total change in biomass accumulation due to growth and recruitment minus mortality; (2) accumulation due to recruitment; (3) accumulation due to growth; and (3) biomass loss due to mortality. For each tree, we transformed diameter measurements per stem into above ground biomass (AGB) using wood density data collected from the literature (Chave et al. 2009), and by employing a global multispecies allometric equation that accounts for bioclimatic stress (Chave et al. 2014). For trees with multiple stems, we calculated the biomass for each stem and then summed the biomass of those stems. Finally, we summed the AGB of all the individuals per plot and calculated the relative plot-level change in biomass between years using the equation of Fisher (1921):

$$\text{Biomass Relative Growth Rate} = \frac{(\ln AGB_{\text{year1}} - \ln AGB_{\text{year0}})}{\text{year1} - \text{year0}}$$

To calculate biomass accumulation independent of recruitment, we selected only those individuals that were measured in the first census and alive throughout the study period. To calculate biomass loss, we summed the AGB of the dead individuals per plot in the census before mortality occurred, and calculated the log difference with the aforementioned equation.

To test whether liana removal influenced tree biomass relative growth rate on all three sources of biomass, we tested four models. In the first model, we evaluated whether lianas (presence/absence), forest age, and mean annual precipitation influenced plot-level relative biomass growth rates. In the second model, we replaced presence/absence of lianas by initial liana biomass (no liana biomass in removal plots and total liana biomass in control plots). In the third model, we retained liana presence/absence and replaced forest age with initial tree and liana biomass (hereafter forest biomass); initial stand biomass can be an accurate proxy of successional changes in stand structure and environmental conditions compared to forest age (van Breugel et al. 2006; Chazdon et al. 2007). In the fourth model, we used initial liana biomass, forest biomass and mean annual precipitation. We tested all four models for all trees combined, and per size class (large trees: DBH > 10 cm, medium sized trees: 5 cm > DBH < 10 cm, small trees: 1 cm > DBH < 5 cm).

To evaluate the effect of liana removal, liana biomass, forest age, initial biomass, and mean annual precipitation (fixed factors) on biomass relative growth rates for each source of biomass, we used Linear Mixed Models (LMM; function lme), as implemented in the R package "nlme" (Pinheiro et al. 2018). We standardized each fixed factor by twice its standard deviation (Gelman 2008). To avoid pseudoreplication, we nested plots within sites in our random effects, and accounted for temporal autocorrelation using the corAR1 structure because our censuses were performed on regular intervals (Gałecki and Burzykowski 2013). We compared alternative models using Akaike Information Criteria, and using marginal and conditional coefficients of determination for generalized mixed-effect models (Bartoń 2013). We then selected the model with the smallest AIC, and plotted the estimated coefficient and their 95% CI of all fixed effects.

Finally, we determined whether liana removal varied among tree species identity. To do so, we first calculated biomass relative growth rate between 2013 and 2017 with species that had more than 30 individuals between those two censuses. We then calculated an LMM per species with liana removal and forest biomass as fixed factors (same factors as in the model with the lowest AIC for all trees combined, see above), and retained the aforementioned structure for the random effects. We evaluated the effect of liana removal among species after accounting for forest biomass by plotting the estimated coefficient from the LMM and their 95% CI for liana removal, with all other variables set at their across-site average values. LMM's did not converge for three species that did not have enough replication between treatments or across plots.

Results

Liana density for stems ≥ 1 cm and ≥ 2.5 cm diameter across our plots was 1207 and 411 lianas ha^{-1}, respectively, which is relatively high compared to other dry forests in the neotropics with similar rainfall (DeWalt et al. 2010). Nonetheless, liana removal did not significantly increase rates of biomass accumulation for all trees combined (Fig. 1). Rates of biomass accumulation were higher in the control plots where lianas were present for four of the five years (19.6%, 31.8%, 22% and 0.5% in 2013, 2014, 2016 and 2017, respectively; Fig. 1a). Biomass accumulation was higher in the liana-removal plots (20.8%) only in 2015 (Fig. 1a). Liana removal did not significantly influence biomass gain via recruitment (Fig. 1b), growth (Fig. 1c), or loss due to morality (Fig. 1d). Model selection indicated that liana removal, forest biomass and mean annual precipitation had the best fit (Table 1), but the absence of lianas did not significantly increase the rates of biomass accumulation throughout forest

succession across our study period (Online Resource 1: Supplementary Figure 1–3).

We expected lianas to have a stronger negative effect on large trees than small trees; however, we did not find a strong negative effect of lianas on any tree size class. For small trees (1–5 cm DBH), biomass accumulation was higher in removal plots between 2013 and 2016 (43.3–198.1%). However, in 2017 biomass relative growth was 124.8% higher in control plots than in removal plots (Online Resource 1: Supplementary Figure 4). Over the entire study period, small trees did not accrue significantly more biomass in the liana-removal plots compared to control plots (Online Resource 1: Supplementary Figure 4). The model with the best fit for small-size trees included liana biomass, forest biomass and mean annual precipitation (Table 1), and it showed that liana biomass had a negative effect on biomass accumulation (Fig. 2). The liana-induced reduction in biomass accretion appeared to be due to higher growth of small trees established in the first census when lianas were present, rather than biomass accumulation of the small trees due to recruitment (Online Resource 1: Supplementary Table 1, Supplementary Figure 4–6).

Liana removal did not significantly increase the rates of biomass accumulation of medium (5–10 cm DBH) or large (> 10 cm DBH) trees (Fig. 2). Rates of biomass accumulation for medium-size trees in 2015 was 115.9% higher in removal plots compared to controls, probably due to high accumulation via recruitment in that year, but the difference across all years was not statistically significant (Fig. 2, Online Resource 1: Supplementary Figure 7 and 8). For large trees, the absence of lianas did not have a significant effect on the rates of biomass accumulation in any census and across censuses, or even after excluding recruitment from growth (Fig. 2, Online Resource 1: Supplementary Figure 9–11). The models with best fit for medium and large trees included liana biomass, forest age, and liana removal and forest biomass, respectively (Table 1). Again, the absence of lianas did not have a significant positive effect on the rates of biomass accumulation due to growth. After excluding recruitment and isolating growth, liana removal did not influence rates of biomass accumulation for medium and large trees (Online Resource 1: Supplementary Table 1 and 2, Supplementary Figure 1, 2, 7–12). In addition, the change in biomass accumulation (growth plus recruitment minus mortality) decreased with forest age for all trees combined as well as for large and medium sized trees (Fig. 3), but biomass accumulation rates between removal and control plots was always similar (Online Resource 1: Supplementary Figures 13–15).

We expected lianas to have a strong positive effect on biomass loss due to tree mortality; however, we did not find a significant effect of lianas on biomass loss on medium and small trees, or on all trees combined (Fig. 1c, Online Resource

Fig. 1 Forest biomass change in control (gray) and in liana-removal plots (white) over five years in a chronosequence of secondary dry forests in the Azuero peninsula, Panama. Data for all 13 plots in each treatment are shown; means (black diamonds) for comparison. Biomass change measured as **a** growth plus recruitment (total biomass changes), **b** Recruitment only; **c** growth only; and **d** loss due to mortality. Recruitment and mortality were measured beginning in 2014, one year after the experiment was established
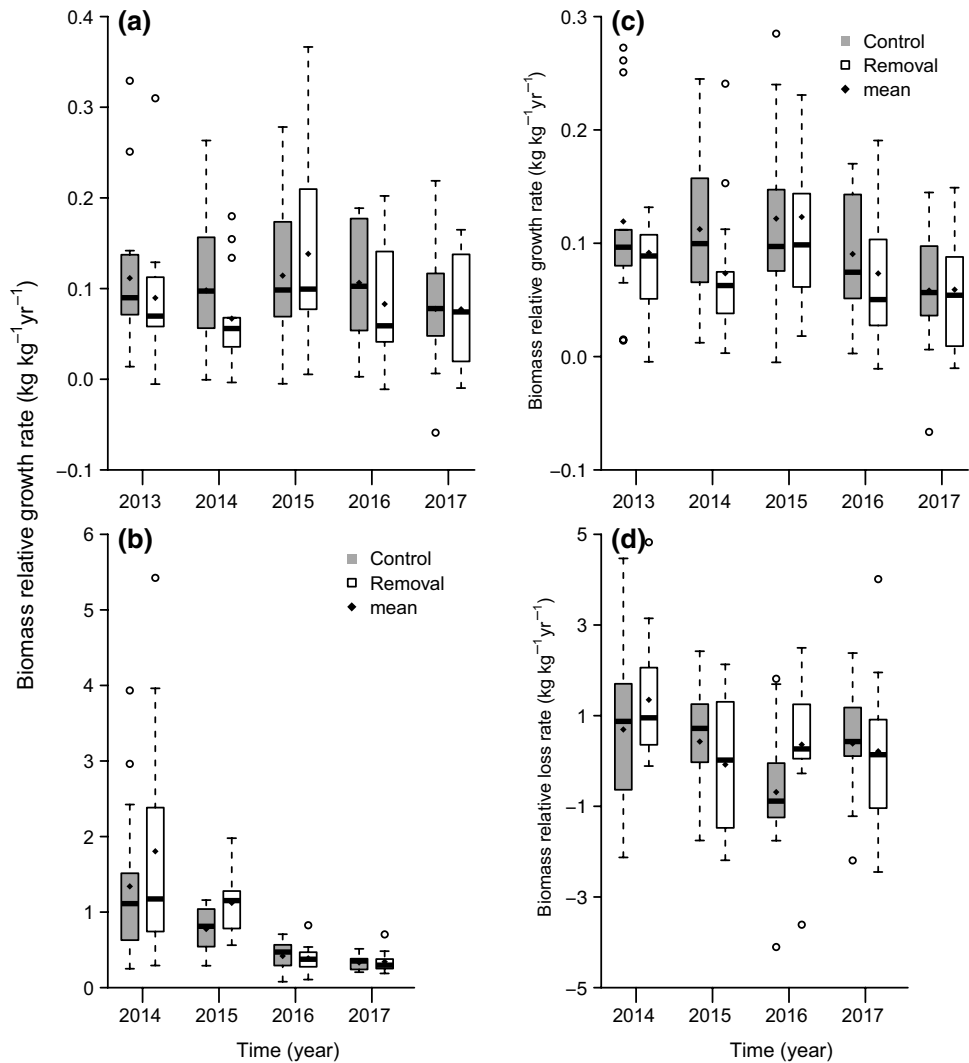
1: Supplementary Table 3, Supplementary Figure 3, 16–17). Very few large trees died during our experiment, therefore we were unable to evaluate how lianas affected biomass loss for this size class.

Of the 41 species that had more than 30 individuals throughout the study, no tree species had greater relative growth rates following liana removal and three tree species had lower relative growth rates following liana removal (compared to controls): *Albizia adinocephala, Bursera simaruba* and *Handroanthus ochraceus* (Fig. 4). Lianas also had a negative effect on the tree species *Guapira costaricana*, but only in the small-size class (Online Resource 1: Supplementary Figure 18–20).

Discussion

Our study is the first experimental quantification of the effects of lianas on tree biomass accumulation, including biomass loss, in regenerating tropical dry forests. We found that lianas neither reduced relative biomass accretion nor increased biomass loss across young secondary tropical dry forests. Although the tree community accrued significantly more biomass in liana-removal plots during some years, the negative effect of lianas was not consistent throughout all years. As a result, tree biomass accumulation was not significantly different in removal plots

Table 1 Results of Linear Mixed Models for biomass relative growth rates (i.e. total biomass change) of all trees, large trees (diameter at breast height DBH > 10 cm), medium trees (5 cm > DBH < 10 cm) and small trees (1 cm > DBH < 5 cm) in 13 control plots and 13 liana-removal plots during five years across a chronosequence of secondary dry forests in the Azuero peninsula, Panama

Tree size class	Model	AIC	R(m)^2 (%)	R(c)^2 (%)
All trees	Liana removal—Age	− 398.8648	35.7	72.9
	Liana biomass—Age	− 398.3936	35.4	72.9
	Liana removal—Forest Bio	**− 399.0723**	**31.2**	**71**
	Liana biomass—Forest Bio	− 398.1759	30.7	71.2
Large trees	Liana removal—Age	− 150.8686	19.2	65.9
	Liana biomass—Age	− 150.8035	19.2	65.8
	Liana removal—Forest Bio	**− 151.4780**	**16.9**	**64.7**
	Liana biomass—Forest Bio	− 151.2658	16.7	64.5
Medium trees	Liana removal—Age	− 226.4561	20	29.4
	Liana biomass—Age	**− 228.2164**	**21.9**	**31.9**
	Liana removal—Forest Bio	− 225.1523	18.3	28.9
	Liana biomass—Forest Bio	− 226.8922	20.4	31.6
Small trees	Liana removal—Age	− 268.2206	2.6	34
	Liana biomass—Age	− 271.6511	5.2	36.8
	Liana removal—Forest Bio	− 268.2011	2.4	35.3
	Liana biomass—Forest Bio	**− 271.9280**	**5.3**	**38.9**

Every model tested the effect of lianas (Liana removal = cutting/no liana cutting; Liana biomass = no liana biomass/total liana biomass), forest age (Age; Forest.Bio = proxy of forest age), and mean annual precipitation in biomass accumulation. Models with the best fit in bold. AIC = Akaike Information Criteria. R(m)^2 and R(c)^2 stand for marginal and conditional coefficients of determination, respectively
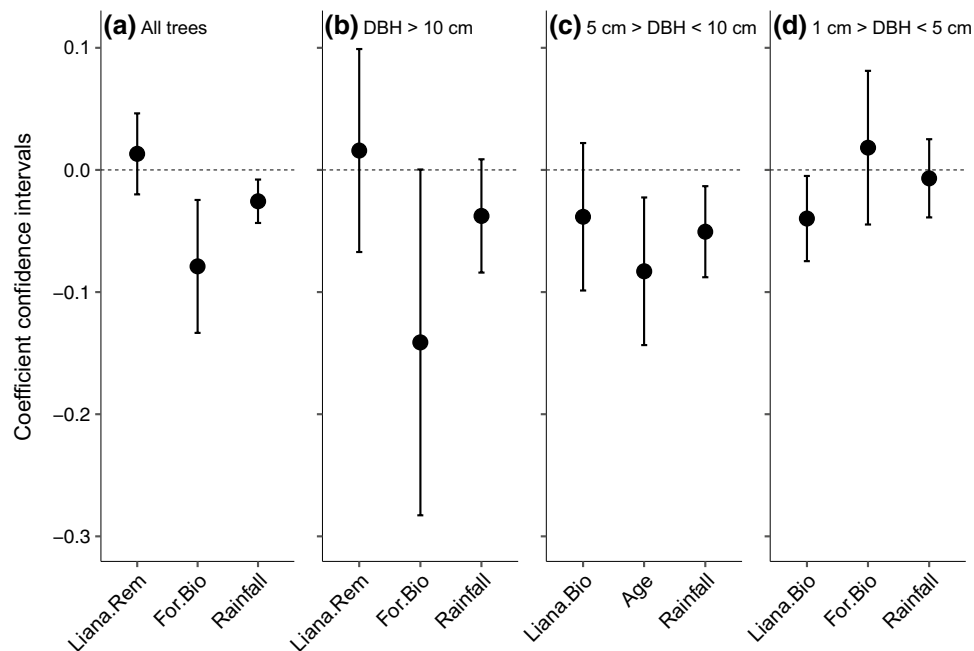

Fig. 2 95% confidence intervals of regression coefficients estimated from linear mixed models to explain tree biomass relative growth rates (i.e. total biomass change) in 13 control plots and 13 liana-removal plots across a chronosequence of secondary dry forests in the Azuero peninsula, Panama. Intervals that do not overlap with zero indicate a strong and significant effect of explanatory variables (e.g. liana removal). Explanatory variables per tree size class were selected from the models with the best fit (Table 1): **a** all trees, **b** DBH > 10 cm represent (large), **c** 5 cm > DBH < 10 cm (medium), and **d** 1 cm > DBH < 5 cm (small). *Liana.Rem* liana removal, *For. Bio* forest biomass, *Liana.Bio* liana biomass, *Age* forest age, *Rainfall* mean annual precipitation

versus control plots after accounting for the effect of forest age and mean annual precipitation. Moreover, lianas did not have a negative effect on the biomass accrued due to
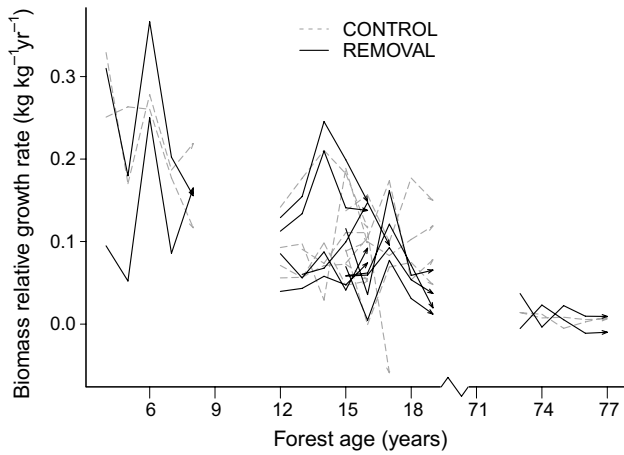
Fig. 3 Trajectories of biomass relative growth rates (i.e. total biomass change) for 13 control plots (gray lines) and 13 liana-removal plots (black lines) during five years across a chronosequence of secondary dry forests in the Azuero peninsula, Panama. Differences between control and removals were not significantly different across forest age (see Fig. 1)

growth (i.e. excluding recruitment), and did not increase biomass loss due to increased mortality.

Results from previous liana-removal studies conducted in dry forests are mixed. For example, in a focal-tree experiment in a Brazilian dry forest, 22 trees of *Swietenia macrophylla* grew faster when lianas were removed compared to control trees, but only after the fifth year of removal (Grogan and Landis 2009). In a dry forest in Bolivia, Pérez-Salicrup (2001) found that lianas reduced seedling growth of *Clarisia ilicifolia* and *Astronium fraxinifolium.* In another focal-tree experiment with four trees of *Swietenia macrophylla* in a Bolivian dry forest site, Barker and Pérez-Salicrup (2000) found that liana removal had no effect on tree stomatal conductance and leaf water potential compared to control trees. In this same forest, however, lianas interfered with tree water availability during the dry season and reduced tree growth for ten individuals of *Senna multijuga* (Pérez-Salicrup and Barker 2000). While the vast majority of liana-removal studies show a substantial negative effect of lianas on trees (Estrada-Villegas and Schnitzer 2018), secondary dry forests might be the exception.

Contrary to our hypotheses, lianas did not have a strong negative effect on biomass accumulation across forest age or among size classes in our study site. We expected that lianas would have a significant negative effect on relative biomass accumulation in younger forests because lianas may have a particularly strong negative effect on small, vulnerable trees. Moreover, we expected that lianas would negatively affect large trees because lianas tend to seek the highest portion of the canopy, which is occupied by large trees (Lai et al. 2017; Estrada-Villegas et al. 2020). However, neither small nor large trees accrued more biomass in the absence of lianas.
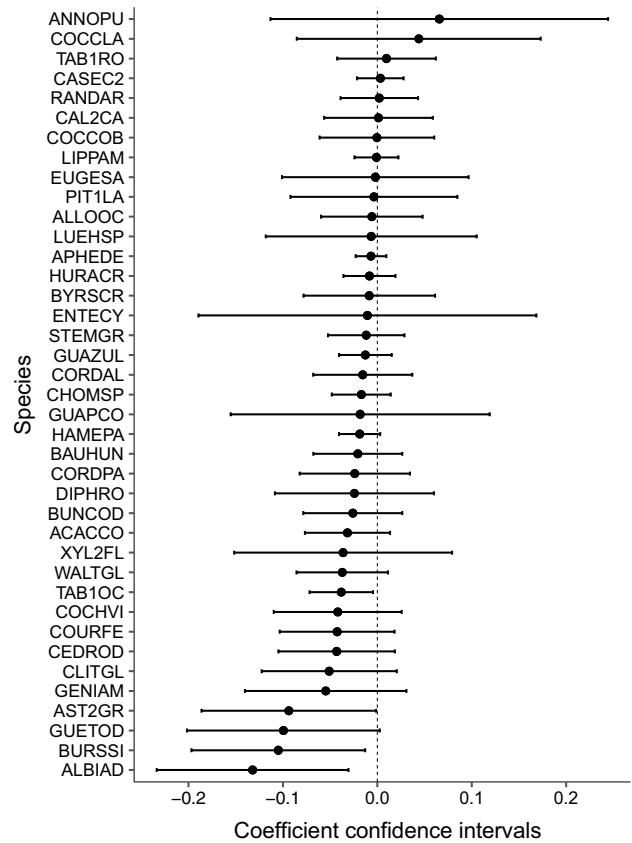

Fig. 4 95% confidence intervals of regression coefficients estimated with Linear Mixed Effects Models for biomass relative growth rates (i.e. total biomass change) between 2013 and 2017 across a chronosequence of secondary dry forests in the Azuero peninsula, Panama. Intervals that do not overlap with zero value indicate a strong and significant effect of liana removal. Species from top to bottom: ANNOPU: *Annona purpurea*, COCCLA: *Coccoloba lasseri*, TAB1RO: *Tabebuia rosea*, CASEC2: *Casearia corymbosa*, RANDAR: *Randia armata*, CAL2CA: *Calycophyllum candidissimum*, COCCOB: *Coccoloba obovata*, LIPPAM: *Lippia americana*, EUGESA: *Eugenia salamensis*, PIT1LA: *Pithecellobium lanceolatum*, ALLOOC: *Allophylus racemosus*, LUEHSP: *Luehea speciosa*, APHEDE: *Aphelandra scabra*, HURACR: *Hura crepitans*, BYRSCR: *Byrsonima crassifolia*, ENTECY: *Enterolobium cyclocarpum*, STEMGR: *Stemmadenia grandiflora*, GUAZUL: *Guazuma ulmifolia*, CORDAL: *Cordia alliodora*, CHOMSP: *Chomelia spinosa*, GUAPCO: *Guapira costaricana*, HAMEPA: *Hamelia patens*, BAUHUN: *Bauhinia ungulata*, CORDPA: *Cordia panamensis*, DIPHRO: *Diphysa americana*, BUNCOD: *Bunchosia odorata*, ACACCO: *Acacia collinsii*, XYL2FL: *Xylosma flexuosa*, WALTGL: *Waltheria glomerata*, TAB1OC: *Handroanthus ochraceus*, COCHVI: *Cochlospermum vitifolium*, COURFE: *Coursertia ferruginea*, CEDROD: *Cedrela odorata*, CLITGL: *Clitoria glaberrima*, GENIAM: *Genipa americana*, AST2GR: *Astronium graveolans*, GUETOD: *Guettarda odorata*, BURSSI: *Bursera simarouba*, ALBIAD: *Albizia adinocephala*

We also expected that the negative effect of lianas on biomass accumulation would be proportional to their density. Again, our data did not support our expectation. Lianas did not reduce biomass accumulation in young forests despite

their high densities, which were 30% greater than the liana density of an old-growth dry forest in Panama (Schnitzer 2005; DeWalt et al. 2010). Mean liana density was 599 individuals per ha in the younger stands, decreasing to 380 individuals per ha in the oldest stands. Despite the high liana densities in young forests, the detrimental effects of lianas were not strong at these forest stands.

We propose four possible explanations as to why lianas did not substantially reduce tree biomass accumulation and did not increase biomass loss in our study. First, trees might have allocated carbon to organs other than stems. Plants allocate more biomass to the organs that will maximize the uptake the most limiting resource (Brouwer 1963). In dry environments where water is a limiting resource, plants should allocate more biomass to roots than to stems (Poorter et al. 2015). Trees in our removal plots might have allocated more biomass to roots so they could absorb the water that was freed by the absence of lianas. In fact, field experiments have shown that tree seedlings allocate more biomass to roots than to stems when competing with lianas (Dillenburg et al. 1993a; Schnitzer et al. 2005). If trees in our experiment increased their belowground biomass at the expense of aboveground biomass, our stem diameter measurements may have failed to capture this differential allocation.

Second, trees and lianas might be partitioning the soil volume differently based on rooting depth, thus reducing competition for water. Recent findings from a dry forest in Costa Rica indicate that lianas have shallower roots compared to trees, and trees with deeper roots might cope better with low water availability (Smith-Martin et al. 2020). In a comparative study of liana and tree rooting depth in a common garden in Panama, however, lianas and trees had similar rooting depth, although lianas appeared to explore more soil volume per stem diameter (Smith-Martin et al. 2019). Lianas and trees may also partition soil moisture seasonally. In a 5-year in situ study of liana and tree growth during the wet and dry seasons in a moist forest in Panama, Schnitzer and van der Heijden (2019) reported that lianas grew more during the dry season whereas trees grew more during the wet season, suggesting that they had the capacity to partition resources (van der Heijden et al. 2019). If trees and lianas are partitioning soil moisture due to different rooting depths or seasonal growth preferences, the absence of lianas would have had a small effect on the soil moisture available for trees. Differential rooting depth or seasonal growth responses might explain why trees with and without lianas accumulated and loss similar amount of biomass. However, other studies have shown that lianas and trees compete strongly for belowground resources (Dillenburg et al. 1993a, b; Schnitzer et al. 2005; Chen et al. 2008), so alternative explanations are also plausible.

Third, higher evaporation due to higher irradiance following liana removal can rapidly dehydrate the top layer of the soil. Even though liana removal can increase soil moisture in the short term (Reid et al. 2015), the water that became available after removal could have been quickly lost due to evaporation from the soil surface (Lebrija-Trejos et al. 2011). During the first years of the experiment, evaporation might have been stronger because 18% more light reached the soil surface after lianas were removed (Rodríguez-Ronderos et al. 2016; Estrada-Villegas et al. 2020). During the last years of the experiment, however, tree foliage may have increased to occupy the space that was vacated by lianas (Rodríguez-Ronderos et al. 2016; Estrada-Villegas et al. 2020), possibly reducing incoming light and thus reducing the loss of moisture due to evaporation.

Fourth, it is possible that lianas have a negative competitive effect on tree biomass accumulation only when trees are not limited by low water availability—during periods of higher water availability (Brown and Lugo 1982; Murphy and Lugo 1986; Becknell et al. 2012). By contrast, during periods of lower water availability, especially in dry forests, both lianas and trees might be too limited to compete (Grime 2002). If this is the case, the interaction between trees and lianas might have a gradient of intensity between moist and dry forests. In moist forests, competition is strong both in wet and dry seasons (van der Heijden et al. 2019), but in dry forests competition might be moderate during wet seasons, and weak during the dry seasons. When enough water is available for trees to grow, lianas compete with trees, but when water is scarce, tree growth is minimal and competition becomes attenuated. Thus, lianas may have had a relatively weak net effect on biomass accumulation because trees had a low capacity to grow for much of the year.

In conclusion, lianas did not reduce tree biomass accumulation in these young tropical dry forests. Our study contrasts strongly with other liana-removal studies, most of which were conducted in moist tropical forests, including early successional moist forests (Estrada-Villegas et al. 2020). Our list of non-mutually exclusive potential explanations include that lianas had no net effect on tree biomass accretion because tree might have allocated biomass to other organs different than stems, trees and lianas partition soil moisture via rooting depth or by seasonal growth, the water not used by trees was quickly lost from the system because of elevated evaporation (when lianas are absent), and the lack of water in this forest weakened the competitive effect that lianas have on trees. A water-addition experiment while measuring stem and root biomass accumulation may help elucidate whether water availability regulates the strength of liana-tree competition in tropical dry forests.

Author contribution statement SE-V, JSH, MvB and SAS conceived and designed the experiment, SE-V, JSH, MvB and SAS collected the data, and SE-V, JSH, MvB and SAS contributed to write the manuscript.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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