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Lianas suppress tree regeneration and diversity in treefall gaps

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Abstract

Treefall gaps are hypothesized to maintain diversity by creating resource-rich, heterogeneous habitats necessary for species coexistence. This hypothesis, however, is not supported empirically for shade-tolerant trees, the dominant plant group in tropical forests. The failure of gaps to maintain shade-tolerant trees remains puzzling, and the hypothesis implicated to date is dispersal limitation. In central Panama, we tested an alternative 'biotic interference' hypothesis: that competition between growth forms (lianas vs. trees) constrains shade-tolerant tree recruitment, survival and diversity in gaps. We experimentally removed lianas from eight gaps and monitored them for 8 years, while also monitoring nine un-manipulated control gaps. Removing lianas increased tree growth, recruitment and richness by 55, 46 and 65%, respectively. Lianas were particularly harmful to shade-tolerant species, but not pioneers. Our findings demonstrate that competition between plant growth forms constrains diversity in a species-rich tropical forest. Because lianas are abundant in many tropical systems, our findings may apply broadly.

Introduction

Periodic disturbances maintain plant species diversity in many ecosystems. In tropical forests, treefall gaps are one of the most common and important disturbances, and saplings in the understory, which capitalize on light or other resources in gaps, depend on gap formation to reach the canopy. Gaps are hypothesized to maintain species diversity via two key mechanisms. First, gaps extend forest resource gradients by providing a high-light resource-rich regeneration niche for some tree species, preventing their competitive exclusion by more shade-tolerant species; evidence for this mechanism is convincing, but only for pioneer tree species (**Brokaw 1985a, 1987**; **Brokaw & Busing 2000**; **Schnitzer & Carson 2001**; **Schnitzer *et al.* 2008a**). The maintenance of pioneer tree species diversity, however, provides only limited support for the gap hypothesis because pioneers typically constitute only a small proportion of the tree species and individuals in tropical forests (e.g., **Dalling *et al.* 1998**; **Hubbell *et al.* 1999**; **Schnitzer & Carson 2001**). Second, gaps may maintain diversity by providing a heterogeneous and resource-rich environment in which different tree species partition resources (e.g., **Ricklefs 1977**; **Denslow 1987**). Within- or among-gap heterogeneity may permit the coexistence of tree species that compete best at some unique combination (or ratio) of resources within a gap or among gaps of different sizes and ages (**Brokaw 1987**; **Brokaw & Busing 2000**; **Schnitzer *et al.* 2008a**). Although, gaps provide a more heterogeneous environment in tropical forests than non-gap sites (**Chazdon & Fetcher 1984**; **Lieberman *et al.* 1995**), there is little empirical evidence that this heterogeneity is important to shade-tolerant trees [reviewed by **Brokaw & Busing (2000)**, **Schnitzer *et al.* (2008a)**]. It remains puzzling why the diversity of shade-tolerant trees, which comprise the vast majority of all tree species, is not maintained by gaps when the critical limiting resource (i.e., light) is suddenly and dramatically elevated.

One hypothesis for why gaps do not maintain the diversity and abundance of shade-tolerant trees invokes seed or dispersal limitation (**Dalling *et al.* 1998**; **Hubbell *et al.* 1999**). This hypothesis posits that limited seed production or seed dispersal, or both, prevent most tree species from reaching treefall gaps in sufficient numbers for resource partitioning to occur. An alternative and previously untested hypothesis is that interference and competition from non-tree plant growth forms, particularly lianas, prevents recruitment or causes the displacement of tree species that arrive in a gap. Lianas are abundant in most tropical forests (**Schnitzer & Bongers 2002**; **Schnitzer 2005**), where they compete intensely with trees indirectly through resource competition, as well as directly through mechanical stress (**Putz 1984a**; **Pérez-Salicrup & Barker 2000**; **Schnitzer *et al.* 2005**; **Toledo-Aceves & Swaine 2008**). In intact forest, lianas reduce tree growth and fecundity, and increase tree mortality (**Grauel & Putz 2004**; **Wright *et al.* 2005**; **Ingwell *et al.* in press**). The effects of lianas may be magnified in treefall gaps, where lianas are particularly abundant and diverse (**Putz 1984a**; **Schnitzer *et al.* 2000, 2008a**, **Schnitzer *et al.* 2004**, **Schnitzer & Carson 2001**). Nearly all studies on liana–tree interactions in gaps, however, have been correlative or were not designed to evaluate whether long-term competition from lianas is severe enough to alter gap-phase regeneration and thereby constrain the diversity and abundance of tree species within gaps.

While lianas appear to harm most tree species in gaps, they may actually facilitate the growth, recruitment and survival of some tree species or guilds. Both **Putz (1984a)** and **Schnitzer *et al.* (2000)** found a significant positive correlation between liana abundance and pioneers species abundance in gaps, whereas the correlation between lianas and shade-tolerant trees was negative. These positive correlations are unexpected given that lianas can smother gaps, thereby arresting gap-phase regeneration (**Schnitzer *et al.* 2000**). The answer may lie in the degree to which lianas compete with pioneers vs. shade-tolerant species. For example, **Clark & Clark (1990)** reported that < 1% of adult pioneer trees at La Selva Biological Station in Costa Rica had lianas in their crowns, whereas most of the shade-tolerant trees hosted lianas. Pioneer trees may be buffered from the deleterious effects of lianas because pioneers can avoid or shed lianas through fast height growth, monopodial non-branching stems, and large leaves that can dislodge attached lianas (**Putz 1984b**). In contrast, shade-tolerant trees lack these characteristics and are vulnerable to colonization by lianas. Thus, lianas may facilitate pioneer tree regeneration by reducing the recruitment and growth of competing shade-tolerant trees (**Schnitzer *et al.* 2000**). To date, however, we lack long-term experimental tests of whether the presence of lianas is unfavourable to shade-tolerant trees, while at the same time favourable to pioneer species in gaps. If the latter point is true, then gaps may enhance the abundance and diversity of pioneer trees not only because gaps are resource-rich habitats, but also because they are habitats with relatively high liana abundance.

We conducted an 8-year liana-removal experiment on Barro Colorado Nature Monument (BCNM), Panama, in which we followed tree recruitment, growth and mortality in gaps with and without lianas. We tested two main hypotheses. First, lianas reduce overall tree growth, recruitment, and survival in gaps, which results in lower tree density and diversity (richness). If the presence of lianas reduces tree growth, recruitment and survival in gaps, and ultimately reduces diversity, then competition from lianas may help explain why gaps fail to maintain tropical tree species diversity because fewer tree species present limits the potential for resource partitioning. Second, we tested the hypothesis that lianas inhibit shade-tolerant tree growth, recruitment, survival, and diversity in gaps, while facilitating pioneer tree growth, recruitment, survival and diversity. If lianas compete with shade-tolerant trees while concomitantly facilitating pioneer trees, then we should find: (1) lower shade-tolerant tree growth, recruitment, survival and diversity in gaps with lianas than in gaps without lianas; and (2) higher pioneer tree growth, recruitment, survival and diversity in gaps with lianas than in gaps without lianas. To our knowledge, this is one of the first *in situ* experimental studies to evaluate whether competition constrains alpha diversity in a tropical forest, and it may explain why gaps fail to maintain shade-tolerant tree species diversity.

Methods

Study site

We conducted the study on Gigante Peninsula, a protected mainland forest that is located adjacent to Barro Colorado Island and is part of the BCNM. Gigante Peninsula is covered by a mix of early and late secondary seasonally moist lowland tropical forest. Mean annual rainfall is 2600 mm, with a dry season from December until April (**Leigh 1999**). For detailed information on the geology, climate, flora and fauna of the BCNM, see **Leigh (1999)**.

Gap selection, liana removal and vegetation census

In 1997, we located all (17) recent (< 1 year old) natural treefall gaps on the fairly flat, upland central plateau of the peninsula. Gap age was determined by the presence of the fallen tree, and each gap was defined as the area, where a vertical line from the edge of the canopy intersected the ground (**Van der Meer & Bongers 2001**). Because gap edges typically receive far more light and are more heterogeneous than the intact forest (**Van der Meer & Bongers 2001**), we extended our sampling 5 m into the gap edge zone. The gaps varied in length, width, orientation and size; gaps were 145–499 m^2, which comprises the most common gap sizes in tropical forests (**Brokaw 1985b**; **Sanford *et al.* 1986**; **Van der Meer & Bongers 2001**). We paired gaps by size for the purpose of randomly assigning treatments, either liana-removal or un-manipulated control, and the liana-removal and control gaps were statistically indistinguishable in total gap area (ANOVA: $F_{1,15} = 0.26$, $P = 0.62$).

In each gap, we tagged, mapped, measured the diameter, and identified to species all lianas and trees > 1.3 m tall. We determined mean per-gap leaf area index (LAI) 1 month before and 1 month after the liana removal in 13 randomly selected gaps (five liana-removal and eight control gaps) by measuring light 50 cm above the soil surface in three locations in the southern half of each gap (facing directly north) during the early morning and late afternoon using a Li-Cor LAI-2000 leaf area index metre (Li-Cor Biosciences, Lincoln, NE, USA).

We recorded light simultaneously with a second LAI-2000 located outside of the forest on the edge of Lake Gatun to calculate relative LAI compared to open sky. To ensure that our open sky measurements did not intercept forest leaf area, we restricted light measurements to the northern portion of the sky by capping the south-facing half of the light sensors for both gap and open sky measurements.

In the control gaps, where lianas were present, we scored each tree in the census using the following scale: 0 = no lianas in the tree crown, 1 = 1–25% tree crown covered, 2 = 26–50% tree crown covered, 3 = 51–75% tree crown covered, 4 = 76–100% tree crown covered (follows **Wright *et al.* 2005**; Ingwell *et al.* in press). In all gaps, we quantified tree crown exposure to direct light for each tree using the following scale: 1 = no direct light during the day, 2 = < 10% direct light during the day, 3 = 11–90% direct light but with occasional crown shading during the day, 4 = direct exposure all day, but only the top or one side of the crown (i.e., a canopy tree), 5 = direct exposure all day for the entire crown (i.e., an emergent tree; method follows **Clark & Clark 1992**).

We recensused the gaps again in 1998 to quantify tree growth, recruitment, mortality, and the liana infestation and canopy exposure indices, as well as to measure LAI. We then cut all of the lianas in eight of the gaps, while nine gaps remained as controls. We cut lianas near the forest floor using machetes, but we did not attempt to remove the lianas from the trees because of the risk of damaging the tree crowns. In each gap, we cut an average of 109 (±17 SE) lianas comprising 20 (±2 SE) species, and neither liana abundance, diversity, nor basal area differed among removal and control gaps prior to the cutting ($F_{1,15} = 1.99$, $P = 0.18$, $F_{1,15} = 0.56$, $P = 0.47$, and $F_{1,15} = 1.97$, $P = 0.18$, respectively). After the liana cutting, we visited all gaps monthly for the first 2 months and bi-monthly for the next 6 months to monitor the gaps and to cut resprouting liana shoots in the removal gaps. Most liana species resprout vigorously after cutting (e.g., **Putz 1984a**, **Schnitzer *et al.* 2004**); however, after 8 months, the cut lianas were no longer resprouting vigorously, and thus we visited the gaps to monitor them and to cut resprouting liana shoots every 3–4 months between censuses. All gaps were revisited with the same approximate frequency and intensity. We recensused the gaps in years 1999, 2000, 2001, 2003 and 2006 to quantify tree growth, recruitment, mortality and the liana infestation and canopy exposure indices. In early 2006, one of the liana-removal gaps was completely covered by the crown of a newly fallen tree, so we omitted this gap in 2006.

Data analysis

We analysed the effects of liana removal on mean per-gap tree relative growth rate (RGR), tree recruitment, and proportional tree mortality, using a repeated measures random effects mixed model, where both treatment and gap were factors (SAS Institute Inc., Belmont, CA, USA, 2007). RGR was calculated as: $(\ln(\text{diameter}_1) - \ln(\text{diameter}_0))/(t_1 - t_0)$, where diameter_1 was the diameter (mm) of an individual in a given census, diameter_0 was the diameter (mm) in the previous census, and $t_1 - t_0$ was the difference in years between sampling years. RGR was calculated in mm year^{-1} for all individuals present in the study from 1998 to 2006 and we used mean RGR per gap for the analyses. We calculated recruitment as the number of individuals per gap that reached the 1.3 height limit and were not included in the previous census. We calculated proportional mortality for each census period as the number of individuals that died between consecutive censuses divided by the total number of individuals alive in the previous census period. To determine whether lianas have a different effect on trees with different life history strategies, we conducted these same analyses on both pioneer and shade-tolerant tree species separately, using the shade-tolerance classification for trees on Barro Colorado Island (BCI) of **Dalling *et al.* (1998)**. We used *t*-test to compare the total species richness of liana-free and control gaps after 8 years, as well as the mean change in species richness per gap (final richness − initial richness) over the 8-year period. We conducted rarefaction simulations using *Ecosim* to test whether differences in tree species richness between removal and control gaps were due to differences in tree number (**Gotelli & Entsminger 2009**). For each gap, we simulated the number of tree species by randomly drawing 80 individuals from the gap 1000 times. We then used a *t*-test to compare the difference in density-independent species richness estimates per treatment. We calculated the Bray–Curtis index for presence/absence and abundance and Jaccard index for presence/absence for all possible pair-wise gap combinations and compared whether the tree community differed in presence/absence and abundance in the control and liana-free gaps using analysis of similarity (ANOSIM; **Clarke 1993**), after removing singleton species. For all of the above analyses, we transformed our data to normalize the residuals when appropriate.

To test whether tree RGR over the 8-year period varied with varying levels of liana infestation and exposure to light in the control gaps (where lianas were present), we used an ANCOVA with liana infestation and light scores as the factors and stem diameter in 1998 as the covariate for all trees combined, as well as for shade tolerant and pioneer trees separately (SAS Institute Inc, 2007). Following the ANCOVA, we used a Tukey HSD test to distinguish significant differences among the liana and light scores. We used a Wilcoxon Sign-Rank Test to determine whether removing lianas significantly reduced gap-level LAI by testing whether the difference in LAI immediately before and 1 month after liana cutting deviated significantly from zero for the liana-removal and control gaps (SAS Institute Inc, 2007).

Results

Growth, recruitment and mortality

Prior to the manipulation (1997–1998), tree recruitment, growth (RGR), and mortality did not differ between the controls and the gaps, where lianas were eventually removed ($P > 0.1$ for all cases). Over the 8-year manipulation, however, lianas significantly reduced tree growth and recruitment in gaps. Mean tree RGR was higher in liana-free gaps than in control gaps in all five censuses (**Fig. 1**; repeated measures ANOVA: $F_{1,15} = 4.90$, $P = 0.04$), and was, on average, 55% higher in the liana-free plots by the end of the study period. Tree recruitment over the 8-year period was also higher in liana-free gaps ($F_{1,15} = 4.13$, $P = 0.06$), with a 46% higher cumulative increase in newly recruited trees in liana-free gaps compared to control gaps (**Fig. 2**). Tree mortality, however, did not differ significantly among treatments ($F_{1,15} = 0.93$, $P = 0.35$; **Fig. 2**). Thus, the predominant effect of lianas on trees in gaps is the reduction of growth and recruitment rather than survival. Nevertheless, the total increase in trees (recruitment − mortality) was 63% higher in liana-free gaps than in control gaps.

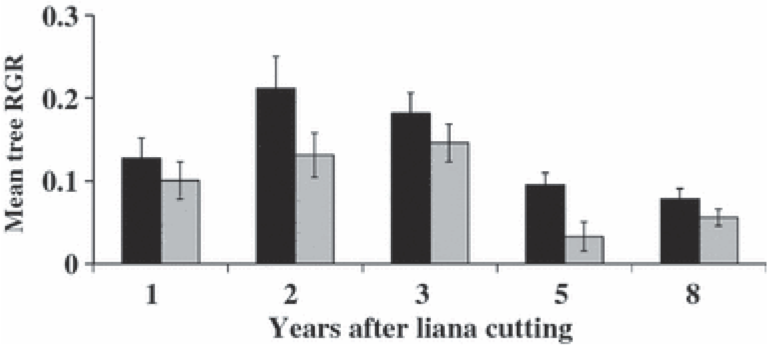

Figure 1

Mean tree relative growth rate (mm year^{-1}) over the 8-year period (1998–2006) in gaps with lianas removed (dark bar on left) and in control gaps with lianas present on Barro Colorado Nature Monument, Panama. Error bars represent one standard error.

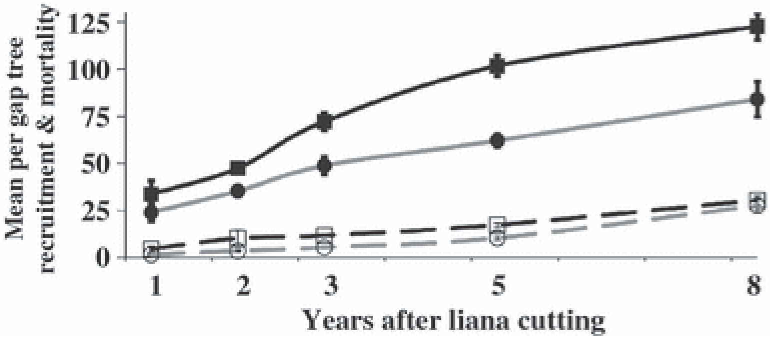

Figure 2
Cumulative recruitment (top two solid lines) from 1998 to 2006 of tree saplings on Barro Colorado Nature Monument, Panama, into the 1.3 m tall size class in gaps with lianas (light lines) and without lianas (dark lines). Bottom two dashed lines represent cumulative tree mortality in gaps with and without lianas. Error bars represent one standard error.

Tree RGR in control gaps decreased sharply with increasing canopy liana infestation ($F_{4,694} = 5.69$, $P = 0.0002$; **Fig. 3a**). This relationship was driven by the significantly higher RGR in trees with no lianas compared to trees with any level of liana infestation (Tukey HSD). Tree growth did not increase with crown exposure to direct light (**Fig. 3b**), although tree growth differed marginally between canopy exposure levels 3 and level 4 ($F_{4,693} = 2.07$, $P = 0.08$). Mean gap LAI decreased 1 month after cutting lianas ($T_S = -6.5$, $P = 0.06$, $n = 5$; Wilcoxon Sign-Rank Test), but did not change in the control gaps ($T_S = -2.0$, $P = 0.42$, $n = 8$), demonstrating that lianas reduced light in gaps (**Fig. 4**).

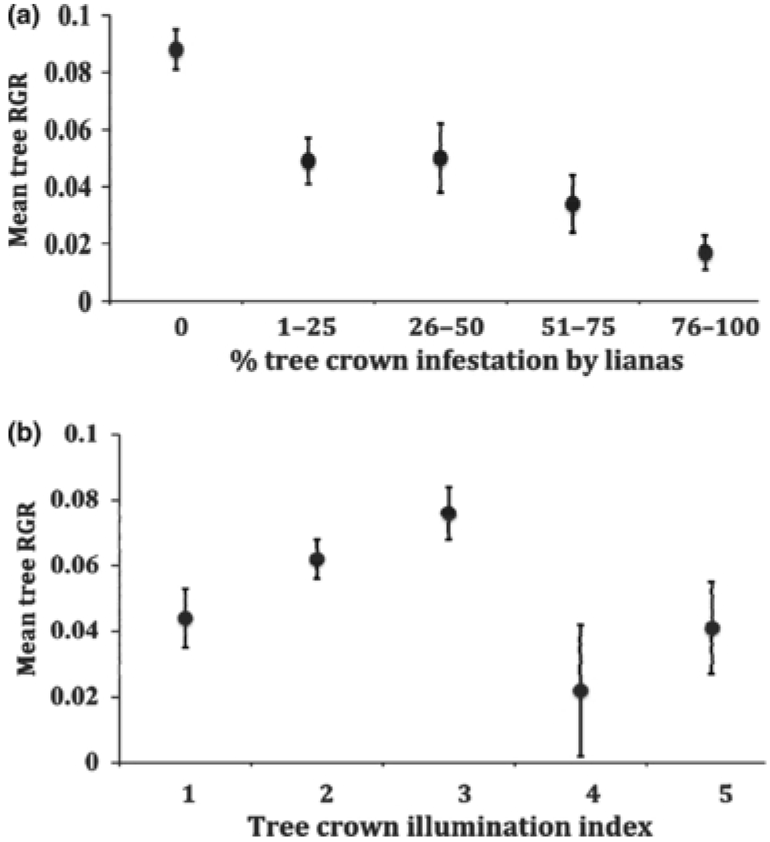

Figure 3
Mean relative growth rates of trees in control gaps (where lianas were present) with varying levels of crown liana infestation (a) and canopy exposure to direct sunlight (b) on Barro Colorado Nature Monument, Panama. Mean tree relative growth rate (RGR) decreased significantly with increasing liana infestation. There was no significant trend in tree RGR with increasing exposure to sunlight, although tree growth differed significantly between tree crown illumination index level 3 and level 4. Error bars represent one standard error.

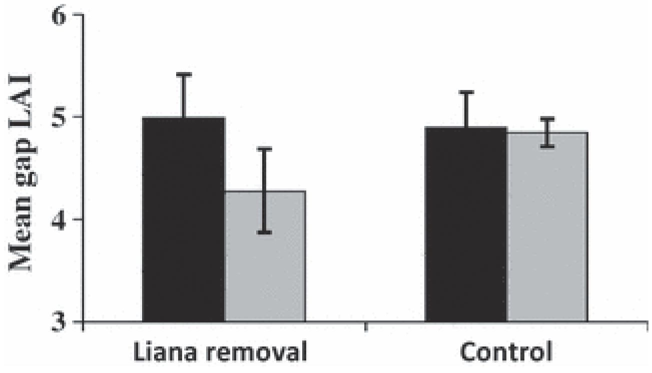

Figure 4
Mean leaf area index (LAI) in liana-removal and control gaps on Barro Colorado Nature Monument, Panama. Dark bars represent LAI before cutting lianas and light bars represent LAI 1 month after cutting lianas. Error bars represent one standard error.

Species richness

Eight years after removing lianas, the increase in mean gap tree species richness (final richness − initial richness) was 65% greater in liana-free removal gaps than in control gaps ($t = 2.16$, d.f. = 11, P =

0.026; Fig. 5). Prior to removing lianas in 1998, tree species richness did not differ between the liana-removal and control gaps ($t = 0.719$, d.f. = 15, $P = 0.24$). After 8 years, tree species richness was marginally higher in liana-free gaps than in the control gaps ($t = 1.44$, d.f. = 14, $P = 0.08$). Rarefaction simulations revealed that the higher species richness in liana-free gaps was due to higher tree density, and richness did not differ in liana-free and control gaps on a per-capita basis ($t = 0.90$, d.f. = 11, $P = 0.19$). Tree community similarity did not differ between liana-free and control gaps (Bray–Curtis: $R = 0.037$, $P = 0.25$; Jaccard: $R = 0.064$, $P = 0.21$), suggesting that the presence of lianas did not alter tree community composition in gaps.

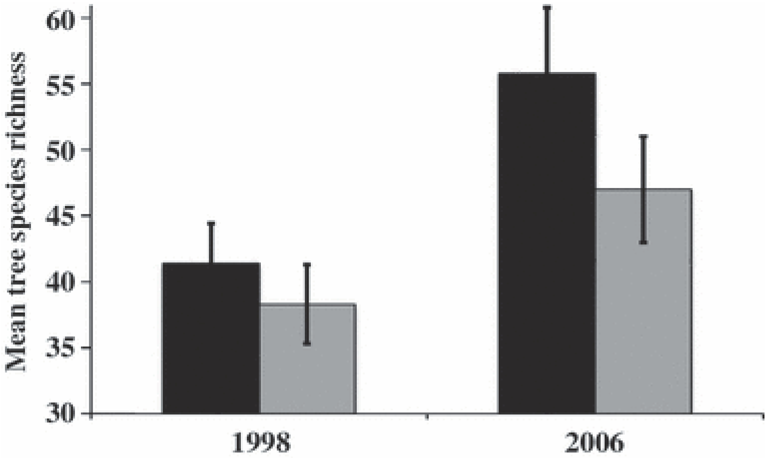

Figure 5

Mean per gap tree species richness in 1998 and 2006 in liana-removal and control gaps on Barro Colorado Nature Monument, Panama. The mean per gap increase in tree species richness was significantly greater in liana-removal gaps (14.4) than in control gaps (8.7). Dark bars represent liana-removal gaps and light bars represent control gaps. Error bars represent one standard error.

Shade-tolerant vs. pioneer trees

The presence of lianas was particularly harmful to shade-tolerant trees, which composed the vast majority of the trees in this study. Mean shade-tolerant tree RGR was 56% higher in the liana-free gaps than in the control gaps ($F_{1,15} = 6.07$, $P = 0.03$). Likewise, mean RGR in the control plots was significantly greater for shade-tolerant trees without liana infestation compared to shade-tolerant trees with lianas in their crowns ($F_{4,619} = 5.49$, $P = 0.0002$). In contrast, pioneer tree RGR did not respond to liana removal ($F_{1,15} = 0.31$, $P = 0.59$), and there was no significant increase in pioneer tree growth with decreasing liana infestation in the control gaps ($F_{4,41} = 1.90$, $P = 0.13$).

The increase in mean shade-tolerant tree species richness from beginning to end of the study was 61% greater in liana-removal gaps than in control gaps (13.0 vs. 8.0 species per gap, respectively; $t = 2.13$, d.f. = 12, $P = 0.027$). The increase in mean pioneer richness over the study period was twice as high in removal gaps than in control gaps (1.43 ± 0.37 vs. 0.67 ± 0.33; Wilcoxon $\chi^2 = 2.82$, $P = 0.09$, d.f. = 1), but the increase was an order of magnitude lower than for shade-tolerant trees. Lianas did not significantly affect recruitment or survival of shade-tolerant or pioneer trees ($P > 0.1$ for all comparisons). Consequently, lianas significantly reduced shade-tolerant tree growth and richness in gaps, slightly reduced pioneer tree richness, and had no discernable effect on pioneer tree growth, recruitment or survival.

Discussion

Competition among contrasting plant growth forms suppresses tree diversity

For more than three decades, gaps were thought to play a major role in the maintenance of woody species diversity in tropical forests (**Ricklefs 1977**; **Brokaw 1985a,b**; **Denslow 1987**). Canopy gaps elevate the key resource limiting growth in the understory (light) and create a highly heterogeneous habitat in the understory in terms of both resources and soil disturbance. Thus, these habitats were thought to be engines of plant recruitment and enhanced performance, particularly for shade-tolerant tree species (**Denslow 1995**). While the maintenance of diversity by gaps has been largely confirmed for pioneer trees and lianas (e.g., **Brokaw 1987**; **Schnitzer & Carson 2001**), it has been rejected for shade-tolerant tree species (**Hubbell *et al.* 1999**; **Brokaw & Busing 2000**; **Schnitzer & Carson 2001**). To date, the primary explanation for why gaps fail to maintain shade-tolerant tree species diversity is because seed and dispersal limitations prevent tree species from arriving in gaps in sufficient quantity for resource partitioning to occur (e.g., **Hubbell *et al.* 1999**; **Brokaw & Busing 2000**). Our results provide an alternative, though not mutually exclusive, explanation: gaps promote the rapid recruitment and growth of lianas, which are inimical to shade-tolerant tree species.

To our knowledge, this is one of the first studies to demonstrate experimentally that interspecific competition between contrasting growth forms can suppress species richness in a tropical forest. Although correlative and short-term experimental studies provide evidence that both palms and lianas compete with trees (e.g., **Putz 1984a**; **Farris-Lopez *et al.* 2004**; **Grauel & Putz 2004**; **Schnitzer *et al.* 2000, 2005**; **Wang & Augspurger 2006**, Ingwell *et al.* in review), our results demonstrate that these competitive effects are severe enough to reduce shade-tolerant tree species diversity over long time periods. Shade-tolerant tree species diversity increased 61% faster in gaps without lianas than in control gaps with lianas. Thus gaps, previously thought to benefit shade-tolerant trees by providing elevated and heterogeneous resources, are also habitats that promote their competitors. Indeed, lianas can become so abundant in gaps that they can completely arrest gap-phase regeneration, resulting in liana-dominated gaps that can remain at low canopy height for decades (**Schnitzer *et al.* 2000**). The relatively high increase in shade-tolerant tree species diversity in liana-free gaps was driven by the increase in density, which we confirmed with rarefaction analyses. By suppressing shade-tolerant tree density in gaps, lianas also suppress shade-tolerant tree diversity, thus limiting the potential number of species that can partition resources. Without sufficient numbers of species arriving and recruiting into gaps, resource partition and niche differentiation among species becomes unlikely, which is the fundamental argument of the seed and dispersal limitation hypotheses, as well as our 'biotic interference' hypothesis. Thus, gaps likely fail to maintain shade-tolerant tree diversity in tropical forests because of a combination of biotic interference from lianas, which constrains shade-tolerant tree recruitment and diversity, as well as seed and dispersal limitations.

Lianas limit tree growth and recruitment in gaps, particularly for shade-tolerant trees

Our experimental findings demonstrate unequivocally that lianas reduce tree growth and recruitment in gaps, presumably by a combination of above and belowground competition, as well as through mechanical stress. Above ground, lianas reduced light in gaps (**Fig. 4**), by increasing the LAI (**Kira & Ogawa 1971**) and wood area index (WAI; **Sánchez-Azofeifa *et al.* 2009**). Below ground, lianas appear to be good competitors for water (**Schnitzer 2005**; **Schnitzer *et al.* 2005**; **Toledo-Aceves & Swaine 2008**), which may limit tree growth in gaps, particularly during the dry season. Lianas cause mechanical stress by adding considerable weight to the tree crown, thus forcing trees to increase stem diameter at the expense of height (**Schnitzer *et al.* 2005**; but see **Toledo-Aceves & Swaine 2008**). Our findings indicate that lianas cause substantial decreases in tree growth rates even when < 25% of the tree crown is covered (**Fig. 3**). Our results are consistent with those of Ingwell *et al.* (in press), who found that liana infestation of trees in the BCI 50 ha plot significantly reduced tree growth and, moreover, that trees with heavy liana infestation were twice as likely to die than trees with few or no lianas in their crowns.

Lianas may also reduce tree recruitment and thus diversity in gaps by increasing the density of seed predators through habitat-mediated indirect effects (*sensu***Royo & Carson 2008**). Lianas provide pathways for mammalian seed predators to traverse the forest canopy and to descend to the forest floor (**Emmons & Gentry 1983**). Dense tangles of lianas, which are common in tropical forests (**Schnitzer *et al.* 2000**), may provide privileged foraging sites for small mammals by providing cover and protecting them from predators (**Emmons 1982**). In many forests, small mammal abundance is positively correlated with liana density (e.g., **Lambert *et al.* 2006**), and seed predation by mammals increases with liana density (**Kilgore *et al.* 2010**). For example, in central Panama, **Kilgore *et al.* (2010)** followed the fate of palm seeds that were placed in the forest and reported that seed removal and predation by mammals increased strongly with increasing liana density. Consequently, lianas not only compete with trees, but they may provide pathways and protected foraging sites for small mammals, which would further limit tree recruitment and diversity in gaps.

Shade-tolerant trees, which comprise the majority of the trees in tropical forests, have life history traits and architectures that make them particularly vulnerable to lianas (**Putz 1984b**; **Schnitzer & Bongers 2002**). These trees tend to grow slowly and deploy many branches to maximize light interception in the forest understory. In gaps, however, these branches provide trellises that lianas use to climb and smother trees, which significantly reduces tree growth even in the high resource gap environment (**Schnitzer *et al.* 2000**).

For pioneer tree species, we found no effect of lianas on growth or recruitment. **Schnitzer *et al.* (2000)** proposed that lianas give pioneer trees a growth advantage in gaps by reducing the growth and abundance of competing shade-tolerant trees. If so, then removing lianas should have decreased pioneer performance. This prediction was not supported by our data. Pioneer tree growth appeared to be invariant to the presence of lianas in gaps, possibly because of the high availability of resources and the ability of pioneers to avoid liana infestation (**Putz 1984b**). Thus, the positive correlation between lianas and pioneer trees in gaps (**Putz 1984a**; **Clark & Clark 1990**; **Schnitzer *et al.* 2000**) may be due to the ability of both groups to capitalize on high resource availability rather than the indirect facilitation of pioneers by lianas.

Distinguishing liana removal from biomass removal

While removing lianas resulted in significant increases in tree growth, recruitment, and diversity in gaps, these types of experiments suffer from the inability to disentangle the effects of liana removal from plant biomass removal. Nonetheless, four lines of evidence suggest that lianas have a disproportionately strong competitive effect on tree growth in relation to their biomass, and that removing an equivalent amount of tree biomass (instead of liana biomass) likely would not have produced the same results. First, lianas have a far higher leaf mass and leaf area to stem diameter (and biomass) ratio than trees, which may allow them to photosynthesize and thus compete more per unit biomass than trees. For example, **Gerwing & Farias (2000)** found that lianas had 4–5 times greater leaf mass per stem diameter than did trees. Second, lianas are able to reach the forest canopy at very small stem diameters (2–3 cm; **Kurzel *et al.* 2006**), where they deploy their leaves and compete for light and soil resources. Trees, in contrast, normally do not reach the forest canopy until they are more than an order of magnitude larger in diameter (**Wright *et al.* 2005**). Thus, unlike saplings, lianas are likely to exert a strong competitive effect even at small size classes. Third, we directly compared the impact of cutting an equivalent biomass of lianas and tree saplings on the performance of neighbouring trees (M. Tobin, A. Wright, S. Mangan, & S. Schnitzer, unpublished data). Neighbouring tree sap-flow velocity (a reliable measure of plant performance) increased significantly immediately after cutting lianas, but did not change after cutting saplings, confirming that lianas can interfere with tree water uptake and photosynthesis, whereas a similar biomass of saplings did not. Fourth, if the growth response from removing lianas in this study had been a biomass effect, the effect should have been relatively short-lived. Plant regeneration in treefall gaps is typically rapid, with gap closure commonly occurring within 6 years of gap formation (e.g., **Brokaw 1987**; **Fraver *et al.* 1998**). If we had witnessed a strict biomass removal effect, the liana biomass that was removed should have been replaced by tree biomass within a few years, and mean tree growth rates in the liana-removal and control gaps should have become equivalent. Instead, tree growth was lower in the control gaps throughout the study, and the effect was particularly strong 2 and 5 years after removing lianas (**Fig. 1**).

Increasing liana abundance: potential community and ecosystem ramifications

Lianas may have strong community- and ecosystem-level effects in forests, and recent studies have reported that lianas may be increasing in abundance and biomass in forests around the world (e.g., **Phillips *et al.* 2002**; **Wright *et al.* 2004**; **Chave *et al.* 2008**; Ingwell *et al.* in press). Liana abundance and biomass may be increasing due to elevated CO_2 or from changes in land-use, forest productivity or rainfall (**Phillips & Gentry 1994**; **Schnitzer 2005**; **Körner 2006**). While the actual causes of liana increases are not yet known (**Körner 2006**; **Schnitzer *et al.* 2008b**), the effects of lianas on forest ecosystems may be substantial. As liana abundance and biomass increase, tree growth, reproduction, survival and diversity will likely decrease in both the intact forest and in gaps (**Wright *et al.* 2005**; Ingwell *et al.* in press). Increasing liana abundance and biomass may ultimately reduce forest tree diversity and forest carbon sequestration because lianas disproportionately displace trees with high wood density (**Schnitzer *et al.* 2000**; **van der Hejden & Phillips 2009**), and liana stems typically contain only a fraction of the carbon in the trees that they displace (**Laurance *et al.* 1997**; **Schnitzer & Bongers 2002**).

Summary

Our findings demonstrate that competition from lianas limits tree establishment, growth and diversity in gaps. While previous studies focused on seed and dispersal limitation as the explanation for why gaps may fail to maintain tree species diversity in general, and shade-tolerant species diversity in particular, our data show that biotic interference and competition from lianas also reduces tree establishment, growth and diversity. The effect of lianas on shade-tolerant trees was particularly strong, whereas lianas appeared to compete relatively little with pioneer trees. If lianas are indeed increasing in abundance and biomass in tropical forests, as reported in other studies, then shade-tolerant tree recruitment, growth, and diversity in gaps will likely decrease, while pioneer tree dynamics may remain largely unaffected.

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