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The impact of lianas on 10 years of tree growth and mortality on Barro Colorado Island, Panama

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Introduction

Lianas are an important component of most tropical forests, comprising 10–45% of the woody species, and typically reaching peak abundance in highly seasonal forests (**Gentry 1991**; **Schnitzer 2005**; **DeWalt *et al.* 2010**). Lianas compete intensely with trees for both above- and below-ground resources (**Dillenburg *et al.* 1993**; **Grauel & Putz 2004**; **Schnitzer, Kuzee & Bongers 2005**; **Chen *et al.* 2008**), reducing tree growth and reproductive output, and altering the relative allocation of stem and leaf biomass (**Putz 1984a**; **Clark & Clark 1990**; **Schnitzer, Dalling & Carson 2000**; **Schnitzer, Kuzee & Bongers 2005**; **Wright *et al.*2005**; **Campanello *et al.* 2007**; **Toledo-Aceves & Swaine 2008a**; **van der Heijden & Phillips 2009**; **Schnitzer & Carson, in press**). By blanketing a tree's crown, lianas likely compete with trees for light, which is limiting in tropical forests, even for canopy trees (**Graham *et al.*2003**). Supporting the weight of lianas may cause mechanical stress in trees, resulting in shorter, thicker trunks (**Schnitzer, Kuzee & Bongers 2005**; but see **Toledo-Aceves & Swaine 2007**). Below-ground competition has also been documented in tropical forests (e.g. **Coomes & Grubb 2000**; **Lewis & Tanner 2000**; **Tanner & Barberis 2007**) and may be particularly common between lianas and trees (**Pérez-Salicrup & Barker 2000**; **Schnitzer, Kuzee & Bongers 2005**; **Toledo-Aceves & Swaine 2007**; **van der Heijden & Phillips 2009**). Thus, lianas potentially compete with trees for below-ground resources, such as water and nutrients, as well as for the position of leaves and light interception in the canopy.

Most studies of liana–tree competition are conducted over relatively short time periods (<5 years), and the longer-term effects of lianas are poorly understood (**Caballe & Martin 2001**; **Phillips *et al.* 2005**). As a result, we lack comprehensive information on how long-term liana infestation, both above- and below-ground, affects the tree growth and survival, and how liana infestation of trees changes over time. Liana infestation might increase steadily once a tree is colonized, remain relatively constant over time or show large oscillations with both increases and decreases in levels of infestation as trees grow. Determining the importance of liana–tree interactions is critical in understanding tropical forest dynamics and may be particularly relevant if lianas are increasing in abundance and biomass, as has been reported for several tropical forests (**Phillips *et al.* 2002**; **Wright *et al.* 2004**; **Wright & Calderon 2006**; **Swaine & Grace 2007**; **Chave *et al.* 2008**).

We examined the impact of lianas on 10 years of tree growth (1995–2005) for 2907 trees of 30 species belonging to various guilds on Barro Colorado Island (BCI), Panama. We quantified tree crown illumination and liana infestation in 1996 and again in 2007, as well as the number and basal area of lianas rooted within 2 m of a subset of these trees in 2007. We also surveyed an additional 3231 canopy trees [diameter at breast height (d.b.h.) ≥20 cm] in 2007 to quantify the level of liana infestation in canopy trees on BCI. We addressed the following questions:

1. How does the level of liana infestation, both in the canopy and on the ground, affect long-term tree growth and mortality?
2. Does the severity of liana infestation and its consequences for tree growth vary with tree species identity and tree crown illumination?
3. How dynamic is the infestation of tree crowns by lianas?
4. Has the proportion of canopy trees infested by lianas increased over the past 40 years?

Materials and methods

We conducted this study in the 50-ha forest dynamics plot on BCI. All trees ≥1 cm diameter were tagged, mapped, measured and identified in 1982, 1985 and every 5 years thereafter (**Hubbell *et al.* 1999**). All rooted lianas ≥1 cm diameter were tagged, mapped, measured and identified in 2007–2008 (**Schnitzer, Rutishauser & Aguilar 2008**). We used these data to locate target trees and to quantify their growth rates over a 10-year period (1995–2005). A complete description of BCI and the 50-ha plot tree and liana census protocols can be found in **Croat (1978)**, **Condit (1998)** and **Schnitzer, Rutishauser & Aguilar (2008)**.

In 1996, we located 2907 target trees (ranging from 4 to 193 cm d.b.h.) of 30 species that differed in maximum mature size and life-history strategy (**Table 1**). For each individual, we quantified crown exposure to direct light (illumination) and liana infestation in the crown. Crown exposure was quantified as either: (i) no direct exposure to light, or (ii) direct exposure to light (follows **Wright *et al.* 2005**). Liana infestation of trees was quantified on a five-point scale, with 0 = lianas absent, 1 = up to 25% of the tree crown covered by lianas, 2 = 26–50% liana cover, 3 = 51–75% liana cover and 4 = 76–100% liana cover (methods follow **Clark & Clark 1990**; **Wright *et al.* 2005**). All measurements were made from the forest floor using binoculars.

Table 1. For 30 tree species on Barro Colorado Island, Panama: life-history information for each species, total number of individuals censused in 1996 and in 2007, the number of additional trees added in 2007, percentage of individuals with lianas in their crown (% liana infestation) in 1996 and 2007, percentage of severe infestation (>50% of crown infested) in 1996 and 2007, and McNemar symmetry chi-square and P-values from contingency analyses of the change in liana crown infestation from 1996 until 2007 (d.f. = 1 for all comparisons; significant changes are in bold)

Species	Family	Life form	Life history	Number of stems (1996)	Number of stems (2007)	Number of trees added (2007)	% Liana infestation 1996	% Liana infestation 2007	% Severe infestation 1996	% Severe infestation 2007	McNemar symmetry chi-square/*P*-value
Alchornea costaricensis	Euphorbiaceae	T	P	132	112	16	90.8	77.7	31.5	39.8	2.94/*P* = 0.08
Anacardium excelsum	Anacardiaceae	T	ST	22	20	0	50.0	40.0	22.7	0.0	0.20/*P* = 0.66
Apeiba tibourbou	Tiliaceae	M	–	27	20	7	62.5	66.6	33.3	33.3	0.20/*P* = 0.66
Astronium graveolens	Anacardiaceae	T	ST	23	20	4	42.1	44.4	19.1	27.8	0.14/*P* = 0.71
Brosimum alicastrum	Moraceae	T	ST	77	64	3	51.3	55.0	27.6	26.7	1.00/*P* = 0.32
Cecropia insignis	Cecropiaceae	T	P	182	135	54	5.6	11.6	0.2	1.8	2.67/*P* = 0.102
Chrysophyllum argenteum	Sapotaceae	T	ST	42	37	3	94.9	90.9	48.7	63.6	1.29/*P* = 0.26
Chrysophyllum cainito	Sapotaceae	T	ST	18	17	1	88.9	81.3	33.3	43.8	0.00/*P* = 1.00
Cordia alliodora	Boraginaceae	T	P	63	50	6	20.6	25.6	0.7	14.0	3.00/*P* = 0.08
Cordia bicolor	Boraginaceae	M	–	307	250	70	72.2	71.0	32.4	49.2	0.05/*P* = 0.82
Dipteryx oleifera	Fabaceae	T	–	32	32	0	21.9	23.3	0.6	10.0	3.33/*P* = 0.56
Eugenia oerstediana	Myrtaceae	M	ST	93	59	49	60.4	63.0	26.4	26.1	1.60/*P* = 0.21
Garcinia intermedia	Clusiaceae	M	ST	403	354	135	59.3	54.6	17.8	13.4	13.79/*P* = 0.000
Hieronyma alchorneoides	Euphorbiaceae	T	P	37	34	1	72.2	63.3	36.1	36.7	0.14/*P* = 0.71
Jacaranda copaia	Bignoniaceae	T	P	193	169	22	19.4	27.0	0.7	12.3	11.84/*P* = 0.001
Laetia procera	Flacourtiaceae	T	–	7	6	0	16.7	20.0	0.0	0.0	0.00/*P* = 1.00
Luehea seemannii	Tiliaceae	T	P	62	54	6	77.1	68.5	47.5	50.0	0.82/*P* = 0.37
Macrocnemum glabrescens	Rubiaceae	M	ST	39	36	6	43.6	71.9	28.2	25.0	0.33/*P* = 0.56
Miconia argentea	Melastomataceae	M	P	188	78	45	68.4	62.1	39.0	40.9	1.09/*p* = 0.30

Ocotea whitei (sigua)	Lauraceae	T	ST	102	81	30	86.3	41.4	30.4	17.1	16.33/*P* = 0.000
Prioria copaifera	Caesalpiniodeae	T	ST	138	132	19	81.6	59.2	24.3	23.8	10.76/*P* = 0.001
Simarouba amara	Simaroubaceae	T	ST	180	112	39	50.0	49.5	28.4	27.2	2.00/*P* = 0.16
Sloanea terniflora	Elaeocarpaceae	T	ST	28	26	1	53.9	69.2	30.8	38.5	1.00/*P* = 0.32
Terminalia amazonia	Combretaceae	T	P	21	20	2	60.0	52.9	10.0	11.8	2.00/*P* = 0.16
Terminalia oblonga	Combretaceae	T	P	36	36	2	33.3	35.3	13.9	17.6	0.67/*P* = 0.41
Trattinnickia aspera	Burseraceae	T	–	23	18	3	21.7	23.5	17.4	11.8	2.00/*P* = 0.16
Trichilia pallida	Meliaceae	M	ST	239	194	45	69.1	63.6	14.4	18.2	4.09/*P* = 0.043
Triplaris cumingiana	Polygonaceae	M	P	147	130	11	20.4	38.9	87.6	15.7	1.00/*P* = 0.32
Virola multiflora	Myristicaceae	T	ST	13	9	3	30.8	25.0	15.4	0.0	0.00/*P* = 1.00
Zanthoxylum ekmanii	Rutaceae	T	P	102	76	30	22.7	38.9	11.3	30.0	10.71/*P* = 0.001

Life form refers to either tall (T, adult height >30 m) or mid-storey (M, 20 m < adult height <30 m) tree species (from Croat 1978). Life history refers to either shade-tolerant (ST) or pioneer (P) (from Croat 1978). We did not attempt to classify species with unresolved life-history attributes.

In 2007, we re-measured liana infestation and crown illumination for the 2127 surviving individuals using the same methods used by SJW and colleagues in 1996. To evaluate precision and repeatability of the measurements between 1996 and 2007, 104 individuals were scored independently in 2007 by LLI and SJW. We found no systematic bias between the two investigators in tree crown liana infestation scores or crown illumination scores (McNemar symmetry chi-square: $P = 0.998$ and $P = 0.593$, respectively). Furthermore, the liana infestation scores differed by two categories for just 3 of the 104 trials and never differed by more than two categories. Because liana infestation might increase as trees age, we surveyed an additional 613 individuals in 2007 that were not included in the 1996 census. The new individuals were chosen to match the species and d.b.h. of trees surveyed in 1996 that had grown into larger size classes or had died by 2007 to enable comparisons of liana infestation levels for similar-sized trees between the two census periods (**Table 1**).

To evaluate possible effects of rooted lianas on nearby trees, we quantified the number and diameter of all lianas ≥1 cm diameter rooted within 2 m of the trunk for 1086 of the original target trees using the liana measurement protocols recommended by **Gerwing *et al.*(2006)** and **Schnitzer, Rutishauser & Aguilar (2008)**. The 50-ha plot is laid out in 50 contiguous 20 × 500 m columns, and the 1086 trees included all survivors from the 1996 census located in all even-numbered columns. In addition to quantifying the absolute number and basal area of lianas within 2 m of each tree, we also normalized for the area sampled around differently sized trees by calculating liana stem density (stems m^{-2}) and liana basal area density (cm^2 m^{-2}).

In 2007, we assessed the level of crown infestation by lianas in all canopy trees (d.b.h. ≥20 cm) in five 4-ha plots using the same survey methods detailed above. All plots were located on the central plateau of BCI. Two of the plots were in the same old-growth forest as the BCI 50-ha plot and three were in late secondary forest adjacent to the BCI 50-ha plot. Over the full 20-ha area, we assessed a total of 3231 trees (646 ± 32.4 plot; mean ± SE). The plots in the older forest and in the late secondary forest did not differ in canopy tree density (641 ± 55.0 and 650 ± 49.7, respectively) or the proportion of trees with lianas (0.74 and 0.73, respectively).

Data analyses

We examined whether tree mortality from 1996 to 2007 varied with liana infestation in 2007 using a proportional-hazards chi-square test (**SAS Institute 2005**). We used the analysis of variance (ANOVA) to test whether tree growth varied with tree crown infestation by lianas (five categories as described above), tree crown illumination (two categories as described above) and their interaction. Because pioneer tree species tend to grow rapidly and have low levels of liana infestation (**Putz 1984a,b**; **Clark & Clark 1990**; **Schnitzer, Dalling & Carson 2000**), we used a preliminary analysis of covariance (ANCOVA) to control the potentially confounding effect of tree species identity. The response variable was d.b.h. in 2005, the grouping variable was species and the covariate was d.b.h. in 1995. We used residuals from this ANCOVAas the response variable in the ANOVA to evaluate the species-independent effects of crown infestation, crown illumination and their interaction for tree growth. We excluded species with fewer than six individuals, ultimately including 27 tree species for this analysis.

For individuals for which we quantified the density and basal area of lianas rooted within 2 m of trees ($n = 1086$), we used ANOVA to test whether our species-independent measure of tree growth varied with the density and basal area of lianas rooted within 2 m of the tree, tree crown infestation by lianas, tree crown illumination and the two-way interaction terms. To simplify the interpretation of this analysis, we dichotomized tree crown infestation by lianas as either light (score ≤1) or heavy (score ≥2; follows **Wright *et al.* 2005**), and rooted liana basal area as either greater or less than median liana basal area. We included the same 27 tree species as in the previous analysis. For both ANOVAs, we log-transformed growth rates when necessary to normalize residuals, excluded insignificant interaction terms with *P*-values >0.25 and reported results for the reduced models (**Sokal & Rohlf 1995**).

We performed two analyses to determine whether liana infestation increased over the 11-year period. The first used the 2127 trees that survived from 1996 to 2007, 5 × 5 contingency tables corresponding to the liana infestation categories in 1996 and 2007, and the McNemar symmetry chi-square test statistic to evaluate the null hypothesis that liana infestation scores were unchanged between 1996 and 2007. The first analysis was performed for all species combined and for each individual species. The second analysis incorporated the 2127 surviving trees and the 613 individuals first assessed in 2007 to replace trees that had died. The second analysis attempts to control for possible effects of tree size on liana infestation – the 613 new individuals were chosen to match species and size distributions between 1996 and 2007 as closely as possible. The second analysis used ordinal logistic regression with tree d.b.h. as a covariate to compare liana infestation scores of all trees assessed in 1996 and 2007. We conducted all analyses in JMP (**SAS Institute 2005**) or SYSTAT 11 (Systat Software, Inc., Richmond, CA, USA).

Results

Tree mortality and growth vary with liana infestation

Mortality was two times greater for trees with the highest level of liana infestation in their crowns (>75%) than for trees with lower infestation levels (**Fig. 1**). Specifically, 156 of the 371 (42%) trees with severe crown liana infestation (>75%) in 1996 were dead by 2007, whereas only 283 of the 1324 (21%) liana-free trees died during this period (proportional hazards chi-square = 74.45, d.f. = 4, $P < 0.0001$).

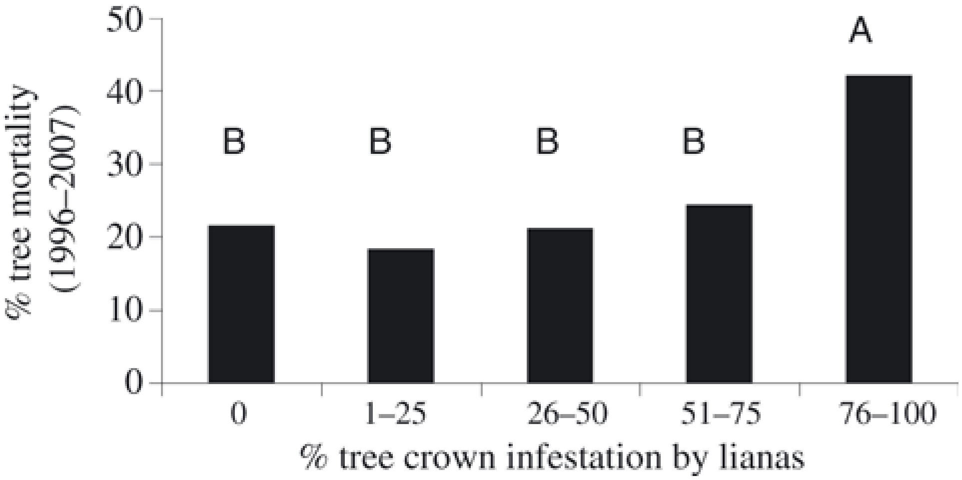

Figure 1 The relationship between tree crown infestation by lianas and tree mortality for 2172 trees over an 11-year period (1996–2007) on Barro Colorado Island, Panama. Trees with severe liana infestation (>75% of the crown) had a significantly higher probability of mortality than all other scored individuals (Proportional Hazards chi-square = 75.45, d.f. = 4, $P < 0.0001$). Different letters indicate significant differences.

Tree crown infestation by lianas significantly reduced the tree growth rate for the 2127 trees that survived from 1995 until 2007 ($F_{4,2201} = 2.38$, $P = 0.047$). Between 1995 and 2005, trees with <50% of their crown covered by lianas grew significantly faster than trees with higher liana infestation ($P < 0.05$, Tukey's HSD). Growth was also significantly higher for trees with sun-exposed crowns ($F_{1,2201} = 97.67$, $P < 0.001$). The interaction between liana infestation and tree crown exposure to sun did not have a significant effect on tree growth ($F_{4,2201} = 0.89$, $P = 0.47$).

In contrast, interactions between liana infestation and tree crown exposure were significant for the subset of 1089 of the 2127 survivors for which the density and basal area of rooted lianas were also assessed (**Fig. 2**). Crown infestation by lianas reduced the growth of trees with sun-exposed canopies but not trees with shaded canopies (**Fig. 2a**; $F_{1,1035} = 11.10$, $P = 0.001$). Growth was lower for trees with more than the median basal area of lianas rooted within 2 m than for trees with less than the median basal area of lianas rooted nearby, particularly for trees with shaded crowns than for trees with sun-exposed crowns (**Fig. 2b**; $F_{1,1035} = 6.28$, $P = 0.012$). Both rooted liana density and basal area increased significantly with canopy liana infestation (**Fig. 3**), making it difficult to tease apart the relative contribution of above- and below-ground effects in this study.

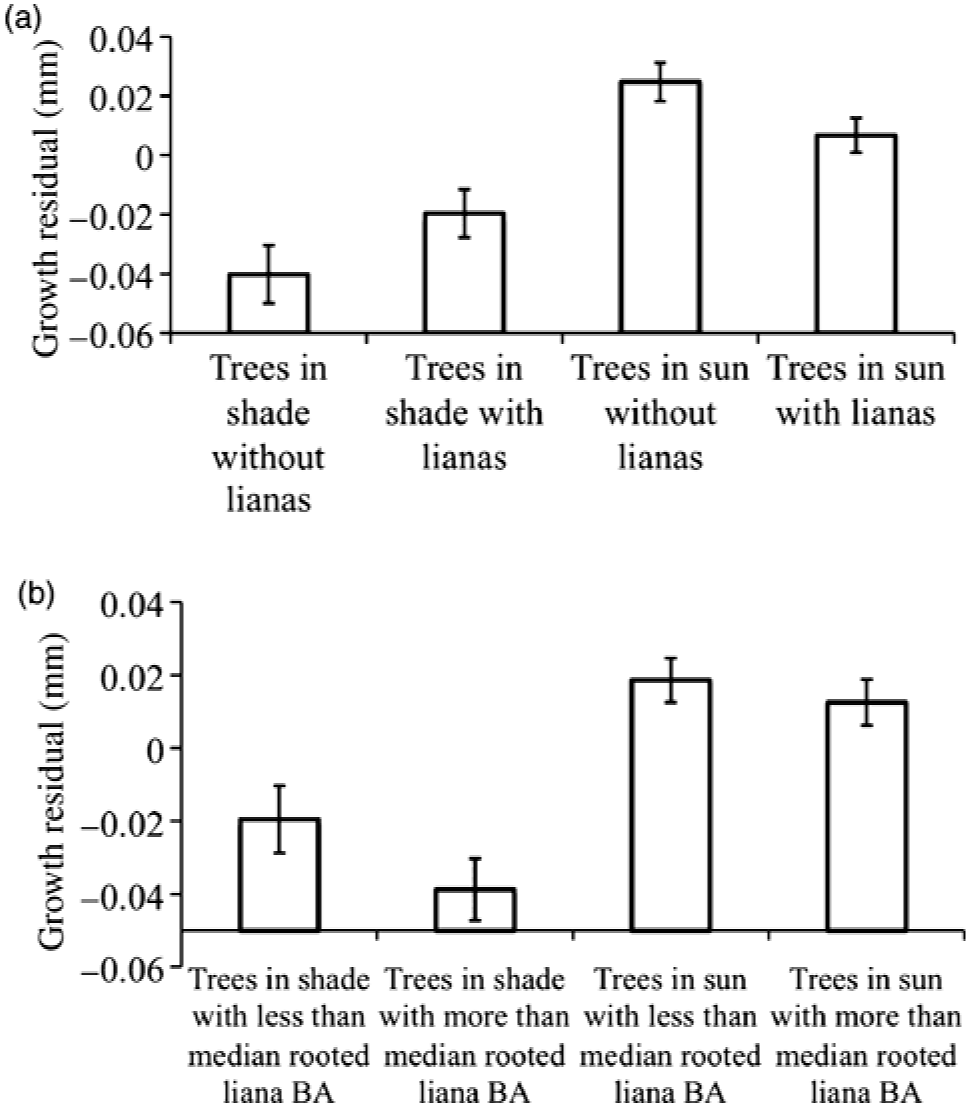

Figure 2 The effects of lianas and crown illumination on tree growth from 1995 to 2005 on Barro Colorado Island, Panama. (a) Growth of shaded and sun-exposed trees with and without lianas in their crown. The significant tree crown exposure × liana infestation interaction ($P = 0.001$) revealed that liana crown infestation reduced the growth of sun-exposed trees, but not shaded trees. (b) Growth of shaded and sun-exposed trees from 1995 to 2005 with above and below median basal area (BA) of nearby rooted lianas (within 2 m of the tree rooting location). The significant tree crown exposure × liana BA interaction ($P = 0.001$) revealed that nearby rooted lianas reduced the growth of shaded trees, but not sun-exposed trees. The

response variable for both panels is a species-independent measure of growth calculated from a preliminary ANCOVA with 2005 d.b.h. as the dependent variable, species as a grouping factor, and 1995 d.b.h. as a covariate.

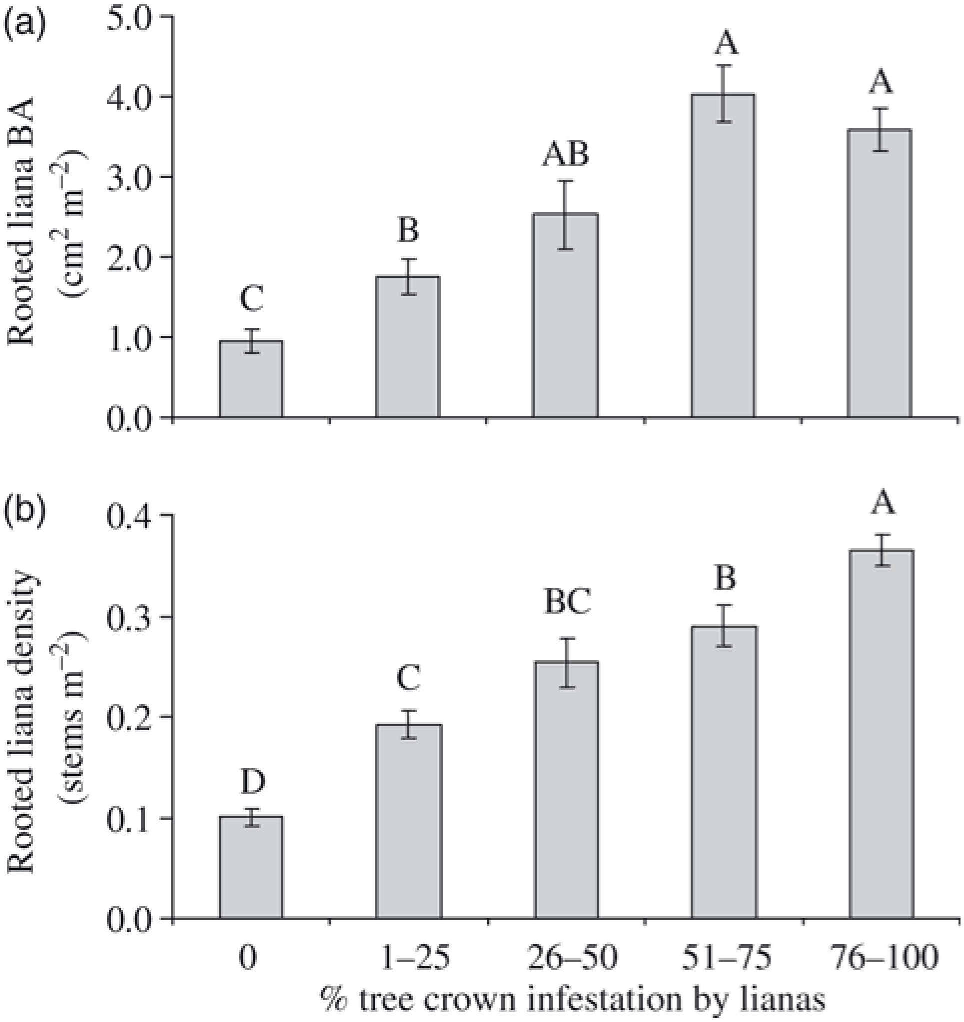

Figure 3 The relationship between the percentage of tree crown liana infestation and (a) basal area density (cm^2 m^{-2}) and (b) stem density (stems m^{-2}) of lianas ≥1 cm rooted within 2 m of trees in the 50-ha plot on Barro Colorado Island, Panama. Rooted liana basal area density and stem density both increased significantly with tree crown infestation by lianas (basal area: $P < 0.0001$, *F*-ratio = 28.94, d.f. = 4; density: $P < 0.0001$, *F*-ratio = 64.63, d.f. = 4). Different letters indicate significant differences.

The prevalence of liana infestation in tree crowns and in soils

Of the 2172 trees of the 30 focal species that survived from 1996 to 2007, 1143 (53%) had at least one liana in their crown in 2007. For the trees for which we quantified both liana canopy infestation and nearby rooted lianas ($n = 1086$), 757 (70%) had at least one liana rooted within 2 m. Seventy-eight per cent of trees had lianas either in their crown or rooted within 2 m of their trunk, whereas only 22% of the trees were completely free of lianas in their crown or rooted within 2 m.

For trees ≥20 cm d.b.h. in the five 4-ha plots, 73.6% ± 3.7 SE had lianas in their crowns in 2007. Across the liana-infestation categories: 26.4% ± 3.7 of the trees were liana-free, 19.6% ± 1.7 had 1–25% crown infestation, 14.8 ± 0.9 had 26–50% infestation, 10.9 ± 0.4 had 51–75% infestation and 28.3% ± 5.3 had severe (>75%) liana infestation.

The 11-year change in liana infestation

Overall, there were significantly more trees with a higher liana infestation score in 2007 than in 1996 (McNemar symmetry chi-square = 118.0, $P < 0.0001$, d.f. = 10). The percentage of trees with the highest level of liana infestation (>75% crown cover) increased by 65% (9.71–15.98%) over the 11-year period (**Fig. 4**, **Table 1**). This large increase was offset by a 54% decrease (15.56–7.14%) in liana infestation in the 26–50% crown cover category, with the other categories changing very little.

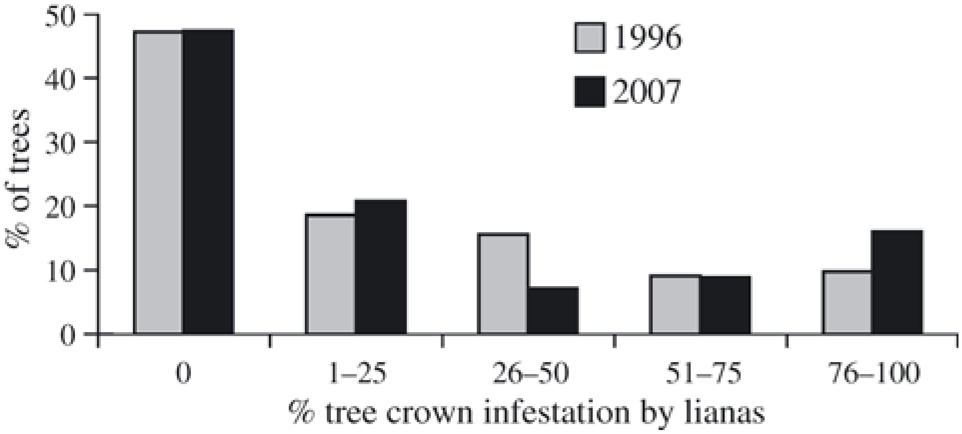

Figure 4 The change in tree crown infestation by lianas from 1996 to 2007 for 2172 trees on Barro Colorado Island, Panama. Tree crown infestation increased significantly over the 11-year period, with a notable increase of 65% (9.71% in 1996 to 15.98% in 2007) for trees suffering severe (>75%) crown infestation.

The increase in liana infestation score for trees in 2007 may have been due to the increase in tree size and age over the 11-year period. We evaluated this possibility by comparing liana infestation scores between all of the original individuals measured in 1996 with trees that survived to 2007 plus the 613 newly added individuals of approximately the same species and size classes as those that died between the 1996 and 2007 censuses (**Table 1**). The increase in liana infestation of crowns was marginally significant (chi-square = 3.32, $P < 0.068$, d.f. = 1). Collectively, these data indicate that liana infestation increased over the 11-year time period, and that this increase was probably not due to increases in tree size or age.

For the majority of the tree species, liana infestation did not change significantly over the 11-year period. However, *Zanthoxylum ekmanii* and *Jacaranda copaia* had significantly higher liana infestation scores in 2007 than in 1996, whereas *Garcinia intermedia*, *Ocotea whitei*, *Prioria copaifera* and *Trichilia pallida* had significantly lower liana infestation scores (**Table 1**).

The modest net changes at the community and species level described above masked the rapid dynamics of liana crown infestation. As one example, 23 of the 211 trees (10.9%) with severe canopy infestation by lianas in 1996 that survived to 2007 were liana-free in 2007. This dramatic change occurred among pioneers (46% of the species, 43% of the individuals), among species with unresolved life-history traits (30% and 35%, respectively) and among shade-tolerant species (23% and 22%, respectively; life-history traits defined in **Table 1**). As a second example, 54 of the 1024 trees (5.3%) with no liana infestation in 1996 were severely infested in 2007. Again, this dramatic change occurred among pioneers (47% of the species, 61% of the individuals), shade-tolerant species (33% and 20%, respectively) and species with unresolved life-history traits (20% and 19%, respectively). Transitions from severe to no liana infestation or from liana-free to severe infestation occurred in trees that ranged from 6.9 to 83.3 cm d.b.h. and 4.1 to 86.7 cm d.b.h., respectively, which included the size range of 96% of the individuals in the study.

Long-term changes in liana infestation

We tested the hypothesis that lianas are increasing in importance by comparing our crown infestation data with previous studies conducted on BCI. In 1980, **Putz (1984a)** quantified liana infestation of canopy trees (≥20 cm d.b.h.) in a series of 100-m^2 plots plus a single 1-ha plot located in the same area as the BCI 50-ha plot and reported that 43–47% of the trees had lianas in their crowns. In 2007 in the five 4-ha plots, we found that 73.6% of trees ≥20 cm d.b.h. had lianas in their crowns – 57% higher than the upper estimate reported by **Putz (1984a)**. In 1967–1968, **Knight (1975)** surveyed 13 stands ranging in size from 0.8 to 2 ha in old growth and late secondary forests on BCI and reported that 32% of the trees ≥10 cm d.b.h. was infested by lianas. Forty years after Knight's study, we found 52.8% of our 30 target tree species ≥10 cm d.b.h. on the BCI 50-ha plot had liana infestation – 65% higher than the percentage reported by **Knight (1975)**. Consequently, our data are consistent with the hypothesis that liana infestation and liana importance are increasing on BCI.

Discussion

The impact of liana infestation on tree growth and survival

Lianas reduced tree growth and survival in the BCI 50-ha plot. In our study, trees with more than 50% of their canopy covered by lianas or more than the median number of lianas rooted nearby had significantly lower growth than did lesser-infested trees. Our findings are consistent with experimental findings that lianas compete intensely with trees (**Pérez-Salicrup & Barker 2000**; **Grauel & Putz 2004**; **Schnitzer, Kuzee & Bongers 2005**; **Toledo-Aceves & Swaine 2008a,b**; **Schnitzer & Carson in press**). Moreover, because trees with heavy liana infestation were twice as likely to have died by the end of the study, our results underestimate the effects of lianas on growth because we omitted the low growth rate of trees that were heavily infested in 1996 but had died by 2007.

Lianas likely compete with trees for both above- and below-ground resources. Above ground, liana leaves displace tree leaves and thus reduces tree photosynthetic capacity (**Kira & Ogawa 1971**). Lianas may also impose considerable mechanical strain on host trees, resulting in lower growth rates, increased allocation to stem thickness at the expense of height and an increased probability of host-tree mortality (**Strong 1977**; **Schnitzer, Kuzee & Bongers 2005**; **Toledo-Aceves & Swaine 2008b**; **van der Heijden & Phillips 2009**). Competition for below-ground resources is also an important form of liana–tree competition (e.g. **Schnitzer, Kuzee & Bongers 2005**; **Toledo-Aceves & Swaine 2007**; **Chen *et al.* 2008**). Because rooted liana basal area, rooted liana density and tree crown infestation by lianas are all positively correlated (Fig. 3), we cannot disentangle above-ground from below-ground effects in this study; however, experimental studies have reported intense below-ground competition between lianas and tree seedlings and saplings (**Schnitzer, Kuzee & Bongers 2005**; **Chen *et al.* 2008**; **Toledo-Aceves & Swaine 2008b**) and adults (**Pérez-Salicrup & Barker 2000**; **Campanello *et al.* 2007**; but see **Barker & Perez-Salicrup 2000**). The strength of each form of competition, however, likely depends on tree species identity (e.g. **Campanello *et al.*2007**), as well as the resources that are most limiting (**Coomes & Grubb 2000**; **Schnitzer, Kuzee & Bongers 2005**).

Consequently, a combination of above- and below-ground estimates of liana competition may provide a more accurate measure of the effects of lianas on tree growth, reproduction and mortality than either estimate alone. Combining both crown infestation by lianas and the presence of nearby rooted lianas increased our estimate of the percentage of canopy and understorey trees interacting with lianas from 53% to 78%. Although rooted liana basal area and the level of tree crown infestation by lianas are correlated, each estimate alone does not fully describe liana–tree competition, and both estimates may be necessary for a comprehensive assessment of liana–tree interactions.

Liana infestation of trees is widespread in tropical forests

Our estimates of 53% of the 30 target tree species in the BCI 50-ha plot and 73.6% of all trees ≥20 cm d.b.h. in the five 4-ha plots having at least one liana in their crowns are consistent with levels of liana infestation reported for other lowland tropical forests (e.g. **Putz 1983, 1984a**; **Campbell & Newbery 1993**; **Alvira, Putz & Fredericksen 2004**; **Grauel & Putz 2004**; **Pérez-Salicrup & de Meijere 2005**; **van der Heijden, Healey & Phillips 2008**). For example, in Danum Valley in Sabah, north-eastern Borneo, 57% of the trees ≥30 cm d.b.h. carried lianas in their crowns (**Campbell & Newbery 1993**; see also **Kammesheidt *et al.*2009**). In the Peruvian Amazon, 58% of the trees ≥10 cm d.b.h. hosted at least one liana in their crowns or climbing on their trunks (**van der Heijden, Healey & Phillips 2008**). In a particularly liana-dense forest in Bolivia, lianas were present in the crowns of 86% of the trees ≥10 cm d.b.h. (**Pérez-Salicrup, Sork & Putz 2001**). In West African forests, the proportion of trees infested by lianas can also be high, with infestation rates reaching 80% (**Parren & Doumbia 2005**). Slightly lower levels of liana infestation have also been reported: 42% for trees >10 cm d.b.h. in Rio Negro, Venezuela (**Putz 1983**), and up to 47% for trees >20 cm d.b.h. on BCI, Panama (**Putz 1984a**). Collectively, these data suggest that the majority of trees in lowland tropical forests around the world experience crown infestation by lianas.

Tree species-specific interactions with lianas

Several studies have demonstrated that pioneer tree species tend to have relatively low levels of liana infestation (**Putz 1984a**; **Clark & Clark 1990**; **Schnitzer, Dalling & Carson 2000**; **Carsten *et al.* 2002**; **Schnitzer & Bongers 2002**; **Schnitzer, Mascaro & Carson 2008**). In this study, we also found that the severity of liana infestation varied by species (**Table 1**), but it was not always consistent among trees with similar life-history characteristics. *Anacardium excelsum*, *Dipteryx oleifera*, *Cecropia insignis*, *Cordia alliodora*, *Jacaranda copaia*, *Laetia procera*, *Ocotea whitei*, *Terminalia oblonga*, *Triplaris cumingiana*, *Trattinnickia aspera*, *Virola multiflora*and *Zanthoxylum ekmanii* all had relatively low levels of liana infestation, and only some of these species (*C. insignis*, *C. alliodora*, *J. copaia*, *T. oblonga*, *T. cumingiana* and *Z. ekmanii*) are classified as early successional pioneers (**Croat 1978**). Other tree species (*Alchornea costaricensis*, *Apeiba tibourbou*, *Chrysophyllum argenteum*, *Cordia bicolor*, *Hieronyma alchorneoides*, *Luehea seemannii*, *Miconia argentea* and *Sloanea terniflora*) had exceptionally severe levels of liana infestation, and this high-infestation group included both pioneer and shade-tolerant species (**Table 1**). Furthermore, over the 11-year period, both pioneers and shade-tolerant trees transitioned from severe crown infestation to no infestation, as well as from no infestation to severe infestation. Thus, although some pioneer tree species appear to consistently avoid liana infestation (e.g. **Clark & Clark 1990**), not all pioneers have this capability and, conversely, not all shade-tolerant trees are equally prone to liana infestation.

The dynamic nature of liana infestation

Our data support the idea that lianas are a dynamic component of tropical forests (**Phillips *et al.* 2005**), which has important implications for liana–tree competition. Nearly 11% of the 211 surviving trees with extremely high liana infestation in their crowns (>75% crown cover) in 1996 had no lianas in their crowns by 2007. In contrast, more than 5% of the 1024 trees with no lianas in their crown in 1996 had severe liana infestation (>75%) in 2007. This finding implies that many trees go through cycles of heavy crown infestation by lianas followed by periods of relatively light infestation. Thus, although lianas compete intensely with trees, reducing growth rates, fecundity and survival (**Putz 1984a**; **Grauel & Putz 2004**; **Schnitzer, Kuzee & Bongers 2005**; **Wright *et al.* 2005**; **Kainer *et al.* 2006**), many of these trees may be periodically released from liana infestation because of the relatively rapid turnover of lianas.

By subjecting their host trees to competitive and mechanical stress, lianas may contribute directly to their own dynamism. Heavy liana infestation often results in tree death (**Fig. 1**), which can dislodge lianas from the forest canopy. Lianas may also increase the number of tree falls because they link tree crowns together, and thus a single-falling tree can result in multiple trees and lianas being pulled from the forest canopy (**Putz 1984a**; **Garrido-Pérez *et al.* 2008**). Lianas that are pulled down with the death of their host may also be pulled from neighbouring trees, along with the entangled stems of other lianas, resulting in a temporary loss of liana infestation and increased liana dynamics. Although most lianas do not die when their host tree falls (**Putz 1984a**), it may take them many months or years to climb back into the forest canopy. Thus, the detrimental effects of lianas on trees contribute to the rapid dynamics of liana communities.

Increasing liana infestation over time

Lianas appear to be increasing in importance on BCI – a pattern that is consistent with reported increases in liana abundance in other neotropical forests (e.g. **Phillips *et al.* 2002**; **Chave *et al.* 2008**). In addition to the significant increase in liana infestation from 1996 to 2007, the percentage of trees infested by lianas on BCI increased by 57% since 1980 and 65% since 1967–1968 (**Knight 1975**; **Putz 1984a**). The severity of liana infestation in trees on BCI also appears to be increasing. The number of trees with severe crown infestation by lianas (>75% crown cover) increased 65% from 1996 to 2007, and this percentage would likely have been higher if the mortality rate of the most heavily infested trees had not been twice that of lesser-infested trees. In our five 4-ha plots, more than 28% of the trees had severe liana infestation (>75%) in 2007. These increases in liana infestation are consistent with the *c.* 50% increase in liana leaf litter and flower production reported between 1987 and 2003 on BCI (**Wright *et al.* 2004**; **Wright & Calderon 2006**), as well as with reported increases of *c.* 100% in large liana densities (>10 cm d.b.h.) in western Amazonian forests (**Phillips *et al.* 2002**).

High levels of liana infestation will result in increased tree mortality and reduced tree growth rates, which have important ramifications for tropical forest dynamics. For example, over the past two decades, tropical tree growth rates have been decreasing in some tropical forests (**Clark *et al.* 2003**; **Feeley *et al.* 2007**). On BCI, **Feeley *et al.* (2007)** reported that the growth rate of adults of 79% of the tree species decreased between 1982 and 2005. Potential mechanisms for this widespread decrease include increased temperature, increased rainfall and cloudiness, and global dimming (see **Feeley *et al.* 2007**). The increase in liana abundance, biomass and levels of tree infestation is another potential explanation for slower tree growth and higher tree mortality in tropical forests such as on BCI.

Conclusions

Our study provides strong evidence that lianas reduce tree growth rates, increase tree mortality risk, are dynamic and increasing in importance. Lianas in tree crowns and lianas rooted within 2 m of trees both reduced tree growth rates. The percentage of trees with lianas rooted nearby and also in the tree crown was nearly 50% greater than the percentage of trees with lianas present just in their crown, suggesting that previous studies might have underestimated the potential for tree–liana competition in tropical forests. The heaviest levels of infestation of tree crowns doubled tree mortality risk. Lianas are dynamic because they can rapidly infest liana-free trees, increase host mortality – thus killing their own conduit to the canopy, and also disappear even when their hosts survive. The complete absence of lianas in 2007 from 11% of the trees with the most severe level of crown infestation in 1996 provided dramatic evidence for liana dynamism. Despite rapid liana dynamics, we documented a significant net increase in levels of host crown infestation between 1996 and 2007. This increase rose to 57% between 1980 and 2007 and 65% between 1967 and 2007 in comparisons with earlier studies that used similar methods (**Knight 1975**; **Putz 1984a**). Increasing levels of liana infestation might be contributing to declines in tree growth rates observed over the past two decades on BCI (**Feeley *et al.* 2007**).

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