

Increasing Liana Abundance and Basal Area in a Tropical Forest: The Contribution of Long-distance Clonal Colonization

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ABSTRACT

Recent evidence suggests that liana abundance and biomass are increasing in Neotropical forests, representing a major structural change to tropical ecosystems. Explanations for these increases, however, remain largely untested. Over an 8-yr period (1999–2007), we censused lianas in nine, 24 × 36 m permanent plots in old-growth and selectively logged forest at La Selva Biological Station, Costa Rica to test whether: (1) liana abundance and basal area are increasing in this forest; (2) the increase is being driven by increased recruitment, decreased mortality, or both; and (3) long-distance clonal colonization explains the increase in liana abundance and basal area. We defined long-distance clonal colonization as lianas that entered and rooted in the plots as vegetative propagules of stems that originated from outside or above the plot, and were present in 2007, but not in 1999 or 2002. Our hypotheses were supported in the old-growth forest: mean liana abundance and BA (≥ 1 cm diameter) increased 15 and 20 percent, respectively, and clonal colonization from outside of the plots contributed 19 and 60 percent (respectively) to these increases. Lianas colonized clonally by falling vertically from the forest canopy above or growing horizontally along the forest floor and re-rooting—common forms of colonization for many liana species. In the selectively logged forest, liana abundance and BA did not change, and thus the pattern of increasing lianas may be restricted to old-growth forests. In summary, our data support the hypothesis that lianas are increasing in old-growth forests, and that long-distance clonal colonization is a major contributor.

Abstract in Spanish is available in the online version of this article.

Key words: climate change; Costa Rica; La Selva Biological Station; recruitment; succession; vegetative reproduction.

LIANAS (WOODY VINES) ARE AN IMPORTANT COMPONENT OF TROPICAL FORESTS, comprising 10–45 percent of woody plant individuals and species (Schnitzer & Bongers 2002), and playing a major role in tropical forest dynamics. Lianas reduce tree recruitment, regeneration, growth, fecundity, and survival (Schnitzer *et al.* 2000, 2005, Toledo-Aceves & Swaine 2008, Ingwell *et al.* 2010, Schnitzer & Carson 2010). In addition, lianas may shape tree community composition via competitive interactions because lianas are deleterious to shade-tolerant trees, but have little effect on pioneer trees (Putz 1984, Clark & Clark 1990, Schnitzer *et al.* 2000, Schnitzer & Carson 2010). Recent evidence indicates that, relative to trees, lianas are increasing in abundance, biomass, productivity, and fecundity in Neotropical and subtropical forests (reviewed by Schnitzer & Bongers 2011). For example, liana increases have been reported in the Central Amazon (Phillips *et al.* 2002, Benítez-Malvido & Martínez-Ramos 2003), the Bolivian Amazon (Phillips *et al.* 2002, Foster *et al.* 2008), French Guiana (Chave *et al.* 2008), and in central Panama (Wright *et al.* 2004, Ingwell *et al.* 2010).

Because of the negative impacts of lianas on trees, higher liana abundance and biomass may substantially alter tropical forest composition and dynamics, as well as important ecosystem-level attributes (reviewed by Schnitzer & Bongers 2011, Schnitzer *et al.* 2011). For example, lianas may lower whole-forest carbon storage by reducing tree growth and increasing tree mortality, especially for shade-tolerant trees with high wood density. Because liana stems contain far less carbon than trees, lianas do not compensate for the tree biomass that they displace (*e.g.*, van der Heijden & Phillips 2009, Schnitzer & Bongers 2011, Tobin *et al.* 2012).

The leading hypotheses to explain liana increases include increasing forest disturbance, increasing duration and severity of seasonal drought, and elevated atmospheric CO₂—all of which may be operating simultaneously and synergistically (Schnitzer & Bongers 2011). Increasing forest disturbance would favor lianas relative to trees by creating more edge and gap habitat, where lianas proliferate (Putz 1984, Schnitzer *et al.* 2000, Schnitzer & Carson 2010, Dalling *et al.* 2012). Stronger seasonal drought may benefit lianas because they suffer less water stress and grow more than trees during dry periods (Schnitzer 2005, Cai *et al.* 2009,

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Zhu & Cao 2010), presumably increasing their fecundity, abundance, and biomass relative to trees. Stronger seasonal drought has been linked to decreases in tree density and increases in liana density in both tropical dry and moist forests (Ingwell *et al.* 2010, Enquist & Enquist 2011), as well as decreases in tree growth in tropical wet forests (Clark *et al.* 2010). Elevated atmospheric CO₂ could favor lianas in two non-mutually exclusive ways. First, elevated CO₂ may increase tree growth, productivity and mortality, ultimately creating more treefall gaps and thus indirectly favoring lianas over trees (Phillips & Gentry 1994, but see Clark *et al.* 2010). Second, elevated CO₂ could favor lianas directly by increasing their growth and fecundity more than trees (Hättenschwiler & Körner 2003, Mohan *et al.* 2006), thereby increasing relative liana size and recruitment. Indeed, Wright and Calderón (2006) reported a strong relative increase in liana flower production compared to trees on Barro Colorado Island (BCI), Panama, where liana density and tree infestation have increased considerably over the past 40 yrs (Ingwell *et al.* 2010). Liana seedling recruitment increased 500 percent over a 6-yr period (1993–1999) in an intact forest in the Central Amazon, whereas tree and palm/herb seedling recruitment decreased 62 percent and 85 percent, respectively (Benótez-Malvido & Martónez-Ramos 2003, see also Chave *et al.* 2008).

Another potential and non-mutually exclusive explanation of increasing liana abundance and biomass in Neotropical forests is through long-distance clonal colonization. Compared to trees, lianas have a much greater ability to produce multiple clonal ramets (*e.g.*, Peñalosa 1984, Putz 1984, Schnitzer *et al.* 2000, 2004, Gerwing 2004). For example, nearly one-third of the *ca* 67,500 liana stems (≥ 1 cm diameter) rooted in the Barro Colorado Island (Panama) 50 ha plot were still connected vegetative offshoots of larger rooted lianas (Schnitzer *et al.* 2012). Furthermore, large lianas can extend through the canopy more than 500 m from their initial rooting point, giving them the capacity to disperse clonal stems far away from the mother stem after it is pulled to the ground in tree- or branch-falls (Putz 1984). Lianas that fall from the canopy can divide into numerous ramets that re-root and become independent from their ‘mother’ genet (Putz 1984, Peñalosa 1984, Schnitzer *et al.* 2000, 2004, Gerwing 2004). In some cases, only part of the liana stem will fall to the ground and re-root, while the mother genet remains in the forest canopy (Putz 1984, Schnitzer *et al.* 2012). Clonal colonization may be particularly common in treefall gaps and other disturbances, where up to 90 percent of liana stems can survive the fall of their host tree, and many of these stems will resprout copiously, re-root, and eventually climb back to the forest canopy (Putz 1984, Schnitzer *et al.* 2000, 2004). If the level of disturbance in tropical forests increases due to greater intensity of seasonal droughts, higher atmospheric CO₂, and land-use changes (reviewed by Schnitzer & Bongers 2011), the number of lianas that recruit as clonal stems will also likely increase, possibly explaining the pattern of increasing liana abundance and biomass in Neotropical forests.

We examined the change in liana abundance and basal area in old-growth and selectively logged forests utilizing a long-term liana demographic study at La Selva Biological Station in Costa

Rica. Increasing intensity of seasonal drought and elevated nighttime temperatures are thought to have reduced tree growth at La Selva (Clark *et al.* 2010), but little is known about the change in lianas at this site. We followed the fate of permanently tagged lianas for 8 yrs to test whether: (1) liana abundance and basal area are increasing in a tropical wet forest; (2) the increase is being driven by increased recruitment, decreased mortality, or a combination of these factors; and (3) long-distance clonal colonization explains the increase in liana abundance and basal area.

METHODS

STUDY SITE.—We conducted the study at La Selva Biological Station, a 1600 ha forest reserve in northeastern Costa Rica (10°25′52″ N, 84°00′12″ W; McDade & Hartshorn 1994). La Selva is a lowland tropical wet forest (Holdridge *et al.* 1971) that receives approximately 4000 mm of rainfall annually, with no month receiving less than 150 mm on average (Sanford *et al.* 1994). Mean monthly temperatures vary little during the year and range from 24.7 to 27.1°C (McDade & Hartshorn 1994). The forest at La Selva is primarily old-growth, but it also has areas of young secondary forest as well as small tracts (*ca* 100 ha) that were formerly old-growth forest, but were selectively logged beginning around 50 yrs ago and large trees were harvested up until 1981 when those areas were acquired by the La Selva Biological Station (McDade & Hartshorn 1994, Mascaro *et al.* 2004, D.A. Clark, pers. comm., D.B. Clark, pers. comm.). Soils are lava-derived ultisols, highly leached, and rich in organic matter (Sollins *et al.* 1994). For more information on La Selva see McDade *et al.* (1994) and on our long-term liana sampling plots see Mascaro *et al.* (2004).

SAMPLING PROCEDURE.—In December 1998, we established nine, 24 × 36 m (0.086 ha) permanent plots in a stratified random design. Six plots (OG 1–6) were in old-growth forest and three plots (SL 1–3) in forests that had been selectively logged as recently as 1981 (Mascaro *et al.* 2004, D.A. Clark pers. comm.). Four of the plots (SL 1, SL 2, SL 3, and OG 3) are on the Matabuey soil consociation, whereas five plots (OG 1, OG 2, OG 4, OG 5, and OG 6) are on the Jaguar soil consociation (Sollins *et al.* 1994), but these two soil types appear to have no significant chemical differences between them (Sancho & Mata 1987).

In January 1999, we tagged, mapped, measured the diameter, and identified to species all freestanding and climbing liana individuals ≥ 0.5 cm in diameter (1.3 m from the root) that were rooted in the plots (methods follow Gerwing *et al.* 2006, Schnitzer *et al.* 2008). Liana stems that were not visibly connected to any other individual were considered to be apparent genets (individual lianas that appeared to be genetically distinct individuals; Schnitzer *et al.* 2006). Individuals that were still attached to the mother stem were considered vegetative clones (ramets), and were not included in our estimates of liana abundance and basal area (follows Putz 1984). We did not excavate lianas that may have been connected below ground, and thus we treated separately rooted lianas that were not attached to another individual

in the census as distinct apparent genets (follows Gerwing *et al.* 2006, Schnitzer *et al.* 2006, 2008).

In July 2002 and in January 2007, we remeasured the diameter of all lianas in the plots, and tagged, mapped, and identified all new lianas that recruited into the 0.5 cm minimum diameter size class. We analyzed the data both inclusive and exclusive of the 0.5 cm stems, but we report stems ≥ 1 cm diameter to make our data more comparable to other studies (recommended by Gerwing *et al.* 2006, Schnitzer *et al.* 2008), as well as to focus on the more stable liana community comprised of larger stems, which have much lower turnover than stems < 1 cm diameter. We classified clonal colonization as lianas that met the following three criteria: (1) were present in the census in 2007, but absent in 1999 or 2002; (2) had clearly entered and rooted in the plot as a part of a stem originating from above or from outside the plot; and (3) were ≥ 2 cm diameter in 2007. Our size criterion was based on the finding that lianas ≥ 2 cm in diameter have an 85–90 percent chance of being present in the canopy in other tropical forests (Kurzel *et al.* 2006).

In November 2007, we collected initial data on the trees and shrubs within the plots. We measured tree, shrub, and palm diameters at breast height (dbh), 1.3 m from the ground of all individuals ≥ 1 cm dbh, which we used to calculate tree/shrub basal area and relative liana abundance and basal area in the nine plots. We excluded palms and restricted our study to woody species.

ANALYSIS.—We compared the change in liana stem number and total basal area from 1999 to 2007 for lianas ≥ 1 cm diameter using the Wilcoxon Signed-Rank Test paired by year and with plot as the unit of replication ($N = 9$) (follows Londré & Schnitzer 2006). We used the same test to compare the net change in liana stem number and total basal area over the 8-yr period with and without the lianas that recruited via vegetative reproduction in all forests combined and in the old-growth and selectively logged forests separately. The results of the 2002 census are reported in Mascaro *et al.* (2004).

RESULTS

We tagged and included a total of 1371 lianas that were present in either the 1999 or 2007 census; 487 individuals were present in both censuses. In 2007, after the first census of free-standing vegetation, there were: 2835 trees and shrubs, 144 palms, and 873 lianas (3852 woody stems and palms ≥ 1 cm diameter). Mean tree and shrub stem number combined per plot was 315 (± 19.52 SE), mean palm number per plot was 16 (± 1.91), and mean liana stem number per plot was 69 (± 3.45). Lianas composed 18 percent of all woody stems ≥ 1 cm (17% including palms). Mean tree and shrub basal area per plot was 30.5 (± 2.86) m^2/ha , and mean liana basal area per plot was 1.00 (± 0.08) m^2/ha —representing only 3.2 percent of the total woody plant basal area.

CHANGE IN LIANA BASAL AREA.—Per-plot basal area (BA) for lianas ≥ 1 cm increased significantly from 1999 until 2007 and was

higher in eight of the nine plots ($P = 0.037$, t -ratio = 2.05, $df = 8$) (Fig. 1A). Median liana BA in the nine plots was 0.85 (range: 0.57–1.10) m^2/ha in 1999 and 1.04 (range: 0.59–1.30) m^2/ha in 2007; a 22 percent increase over the 8-yr period. Mean liana BA was 0.86 (± 0.07 SE) m^2/ha in 1999 and 1.00 (± 0.08) m^2/ha in 2007; a 16 percent increase over the 8-yr period. Liana clonal colonization from outside of the plot added a total of 1.10 m^2/ha BA into the nine plots (combined) over the 8-yr period, which constituted 60 percent of the increase in BA of new recruits (Figs. 2A and B).

Liana BA increased significantly from 1999 to 2007 and in all six old-growth plots ($P = 0.02$, t -ratio = 2.76, $df = 5$). Median liana BA increased from 0.97 (range: 0.65–1.16) in 1999 to 1.14 (range: 0.90–1.25) in 2007; a 17.5 percent increase over the 8-yr period. Mean liana BA of the old-growth forest sites was 0.95 (± 0.07) m^2/ha in 1999 and 1.14 (± 0.07) m^2/ha in 2007; a 20

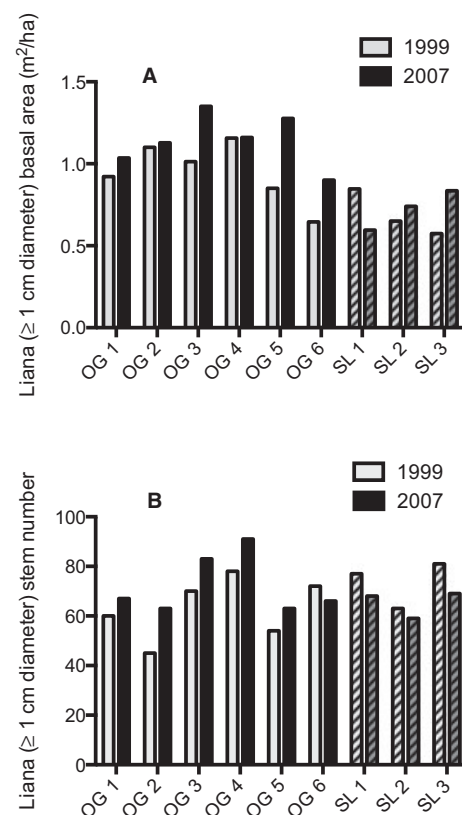


FIGURE 1. Per plot basal area (A) and stem number (B) for lianas ≥ 1 cm diameter in 1999 and 2007 in nine, 24 \times 36 m plots at La Selva Biological Station, Costa Rica. The increase in basal area was significant in the old-growth plots, but not in the selectively logged plots. The increase in liana stem number was significant in the old-growth plots, but not in the selectively logged plots. Plots labeled OG 1–6 (solid bars) were located in old-growth forest and plots labeled SL 1–3 (hatched bars) were in selectively logged forest. Liana basal area was higher in all six of the old-growth plots (BA in OG 4 was higher in 2007 than in 1999—1.157 m^2/ha in 1999 vs. 1.61 m^2/ha in 2007) and liana stem number was higher in five of the six old-growth forest plots.

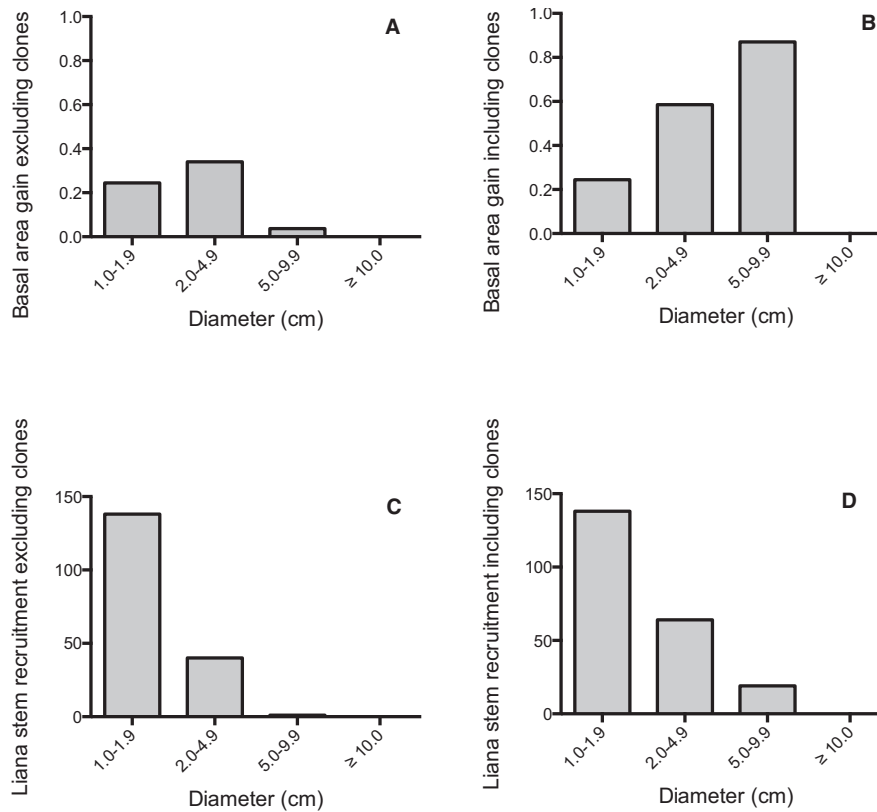


FIGURE 2. Liana basal area and stem recruitment from 1999 to 2007 of all stems combined in nine, 24 × 36 m forest plots at La Selva Biological Station, Costa Rica. Six of the plots were in old-growth and three were in selectively logged forest. Panels A and B represent the total amount of liana basal area that recruited into the plots during the 8-yr period excluding and including clonal colonization, respectively. Panels C and D represent the total number of lianas that recruited into the plots during the 8-yr period excluding and including clonal colonization, respectively.

percent increase over the 8-yr period. In the selectively logged forests ($N = 3$), however, liana BA did not change significantly over the 8-yr period ($P = 0.58$, t -ratio = 0.22, $df = 2$).

CHANGE IN LIANA ABUNDANCE.—Liana abundance did not change over the 8 yrs, and only five of the nine forest plots had more lianas in 1999 than in 2007 ($P = 0.56$, t -ratio = 0.16, $df = 8$; Fig. 1B). Median liana abundance in 1999 and 2007 were 72.0 (range: 45–83) and 67.0 (range: 59–91), and mean liana abundance in 1999 and 2007 were 69.2 (± 4.3) and 69.9 (± 3.5), respectively. Forty-two lianas recruited via clonal colonization from outside of the plots, comprising 19 percent of new recruits ≥ 1 cm diameter (Figs. 2C and D).

Restricting the comparison to the old-growth plots revealed that liana abundance (≥ 1 cm diameter) was significantly higher in 2007 compared with 1999 in five of the six old-growth plots ($P = 0.022$, t -ratio = 2.66, $df = 5$) (Fig. 1B). Median per plot liana abundance in the old-growth plots was 71 (range: 45–83) in 1999 and 66.5 (range: 63–91) in 2007. Mean per plot liana abundance was 67.0 (± 5.0) stems per plot in 1999 and 72.2 (± 4.8) in 2007; a 14 percent increase. Liana abundance in the selectively logged forest did not change significantly from 1999 until 2007 ($P = 0.58$, t -ratio = 0.22, $df = 2$) (Fig. 1B).

LIANA DYNAMICS (MORTALITY AND RECRUITMENT).—Liana mortality was high over the 8-yr period; 41.3 percent (248 stems total) of the individuals died, and this mortality was concentrated (51.2%) in the smallest size class (1.0–1.9 cm). Mean per plot recruitment, however, balanced mortality for the smallest size class; an average of 15 small stems recruited into each plot, whereas 14 small stems per plot died by 2007 (Figs. 3A and B). The greatest increase in liana BA was in the larger size classes (≥ 2 cm diameter), and was driven primarily by clonal colonization from relatively large individuals that originated from outside the plot (Figs. 2A and B and 3C and D). In the old-growth forest, total recruitment for lianas ≥ 1 cm diameter was 15 percent higher than mortality (169 stems vs. 147, respectively). In the selectively logged forest, mortality of lianas ≥ 1 cm diameter was twice as high as recruitment (101 vs. 52 stems, respectively).

DISCUSSION

Our findings support the hypothesis that lianas are increasing in abundance and basal area, and probably also biomass, in the old-growth forest at La Selva. The increase in lianas at La Selva is consistent with similar reports of liana increases in other old-growth Neotropical forests (reviewed by Schnitzer & Bongers

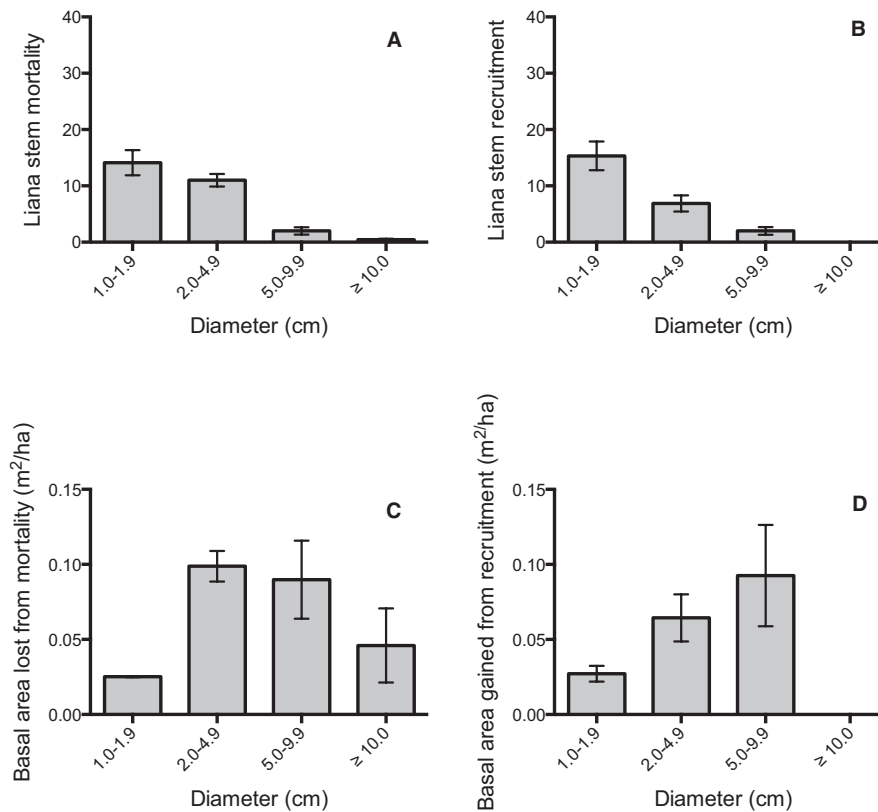


FIGURE 3. Mean liana mortality (A), recruitment (B), basal area lost (C), and basal area gained (D) of all stems from 1999 to 2007 over four size classes in nine, 24×36 m forest plots at La Selva Biological Station, Costa Rica. Six of the plots were in old-growth and three were in selectively logged forest. Mean values were based on all lianas in four discrete size classes (including clonal colonization for size classes ≥ 2 cm diameter) using each plot as a replicate. Error bars represent one standard error.

2011). Mean liana abundance increased 15 percent and basal area increased 20 percent over the 8-yr period in the old-growth forest. The largest increases in liana basal area between 1999 and 2007 were in the 2.0–4.9 cm and 5.0–9.9 cm size classes and were due mostly (60%) to long-distance clonal colonization (Figs. 2 and 3), supporting the hypothesis that long-distance clonal colonization is a driver of increasing liana basal area. Lianas have a far greater capacity for long-distance clonal colonization than trees (Schnitzer *et al.* 2004), and lianas are increasing in Neotropical forests relative to trees (Schnitzer & Bongers 2011). Thus, long-distance clonal colonization provides a compelling explanation for the increase in liana abundance and basal area at La Selva as well as in many other tropical forests (Peñalosa 1984, Putz 1984, Gerwing 2004, Schnitzer *et al.* 2012).

LONG-DISTANCE CLONAL COLONIZATION.—Lianas appeared to colonize the study plots by falling from the canopy and re-rooting following tree- and branch-falls, and there was evidence of tree-falls of varying ages in the old-growth forest during the 2007 census (S. R. Yorke, pers. obs.). The ability of lianas to grow long distances from the initial rooting point and to extend through dozens of tree crowns before falling to the forest floor and re-rooting (Peñalosa 1984, Putz 1984) enables lianas to propagate

clonally far from their point of origin. We term this phenomenon long-distance clonal colonization and suggest that it may be an important form of clonal spread by lianas in tropical forests (see also Peñalosa 1984, Putz 1984). Long-distance clonal colonization may occur in one of two ways. First, a disturbance (*e.g.*, tree or branch fall) can cause a clean break of a large liana branch from its parent and, once on the ground, it re-roots and grows back to the canopy (Putz 1984). Second, lianas may fall to the forest floor, re-root, and produce multiple liana stems while still connected to the parent stem, which remains in the forest canopy (Putz 1984, Schnitzer *et al.* 2004). This latter method of colonization may be particularly effective in allowing lianas to proliferate if the parent stem supplies carbohydrates, water, and nutrients, giving the clonal propagules the resources necessary to become independently rooted lianas that can climb back up to the canopy, even at relatively small stem diameters (Kurzel *et al.* 2006). At some future point, the connection between the clonal propagules and the parent stem may disintegrate, resulting in multiple separate ramets that become independent ‘apparent genets’ (*sensu* Schnitzer *et al.* 2006, 2012). Because of the ability of lianas to course through multiple tree crowns and to resprout copiously in tropical forests in many parts of the world (*e.g.*, Putz 1984, Schnitzer *et al.* 2004, Garrido-Pérez *et al.* 2008), long-distance

clonal colonization is likely to be a common method of liana colonization. Furthermore, if disturbance has increased in tropical forests then long-distance clonal colonization may have also increased, which may contribute to the relative increase in lianas in tropical forests.

Long-distance clonal colonization along the soil surface may also contribute to increasing liana abundance and biomass. Lianas may extend horizontally across the forest floor and establish new rooting points long distances from the original rooting location. At each rooting point, the liana will often create a new stem, and thus a single individual snaking along the forest floor has the capacity to become multiple independently rooted clones, each separated by dozens of meters (Peñalosa 1984, Putz 1984). In the selectively logged forest, we did not find direct evidence of treefalls, but two plots had clonal colonists, suggesting that lianas recruit via long-distance clonal colonization even in the absence of treefalls.

LIANA CHANGES IN SELECTIVELY LOGGED AND OLD-GROWTH FORESTS.—Liana abundance decreased in all three selectively logged forest plots over the 8-yr period—a noticeable deviation from the pattern of liana increases in five of the six old-growth forest plots. Previous logging activity at La Selva within 20 yrs of our initial observations may have increased liana abundance because lianas recruit rapidly into treefall and logging gaps (*e.g.*, Putz 1984, Babweteera *et al.* 2000, Schnitzer *et al.* 2000, 2004, Foster *et al.* 2008). Eventually, however, liana mortality should reduce the number of lianas with the decrease in light, and the decrease in liana abundance in all three selectively logged plots and increase in BA in two of the three selectively logged forests may be a natural successional pattern of declining liana abundance and increasing basal area after logging (Dewalt *et al.* 2000, Letcher & Chazdon 2009). Perhaps, the drivers that caused increases in liana abundance and basal area in the old-growth forest were also operating in the selectively logged forests, but were subordinate to the successional patterns of decreasing lianas and increasing basal area. We cannot evaluate this hypothesis with our dataset.

In the old-growth forest, decreasing dry season rainfall and increasing temperature may drive the increase in lianas—both factors combined increase evapotranspirative demand (Schnitzer & Bongers 2011). Lianas perform relatively better than trees under higher evapotranspirative demand (*e.g.*, Schnitzer 2005), and even though rainfall at La Selva is still relatively high during the dry season (>100 mm per month), even slight changes in rainfall and temperature may significantly affect plant performance (Clark *et al.* 2010). For example, over the past 24 yrs, tree growth at La Selva was significantly lower during periods of reduced dry season rainfall and increased temperature (Clark *et al.* 2010). These changes in climate may also favor the lianas of La Selva by increasing tree mortality and treefall gap formation, which promotes liana regeneration, density, and diversity (Schnitzer *et al.* 2000, 2012). Increasing gap formation also increases long-distance clonal colonization, which appears to be a strong contributor to liana increases at La Selva.

The increase in lianas may be a permanent directional change in tropical forests, or it may be an oscillating trend that would later be balanced by liana decreases. It is possible that we recorded a natural fluctuation in liana abundance, but we have not monitored these plots for long enough to detect a corresponding decrease in abundance. If this possibility is true, however, we should then expect to see a greater balance between large liana recruitment and mortality at the plot level, which is not supported by this study or by other studies that report increased liana abundance and basal area (Phillips *et al.* 2002, Chave *et al.* 2008, Schnitzer *et al.* 2012), leaf litter production (Wright *et al.* 2004), liana floral production (Wright & Calderón 2006), and levels of tree infestation by lianas (Ingwell *et al.* 2010). Furthermore, we selected the plots randomly and without any preconceived notion of forest structure (*e.g.*, we did not avoid gaps); hence, if there are cyclical changes in liana abundance with gap-phase regeneration we would expect to have all phases represented in our plots. If the increases in liana abundance and basal area documented here and elsewhere continue into the future, they indicate marked changes in forest structure (Schnitzer & Bongers 2011), particularly at La Selva and other wet forests where liana abundance and basal area are relatively low in comparison to more seasonal forests (Mascaro *et al.* 2004, Schnitzer 2005, Dewalt *et al.* 2010).

As lianas increase, they have a greater competitive effect on trees, and even a small number of lianas in a tree can reduce its growth (*e.g.*, Schnitzer & Carson 2010, Tobin *et al.* 2012). When liana abundance becomes high, tree mortality increases substantially (Ingwell *et al.* 2010), thus increasing forest turnover and possibly leading to a positive feedback between increasing lianas and tree mortality (Phillips & Gentry 1994). Lianas and fast-growing pioneer tree species with low wood density capitalize on the resulting treefall gaps (Putz 1984, Phillips & Gentry 1994, Schnitzer *et al.* 2000, 2004), and together they may displace slower-growing, shade-tolerant tree species, which have higher wood density (Schnitzer *et al.* 2000, van der Heijden & Phillips 2009, Schnitzer & Carson 2010). If the trend of increasing lianas continues, the liana-mediated restructuring of tree regeneration and survival may ultimately lead to lower overall carbon sequestration in tropical forests because the amount of carbon in lianas and pioneer trees does not offset that in displaced high wood density, shade-tolerant species (Laurance *et al.* 2001, Phillips *et al.* 2002, Schnitzer & Bongers 2002, van der Heijden & Phillips 2009, Schnitzer & Bongers 2011). Consequently, our findings of increasing liana abundance and basal area in the old-growth forests at La Selva represent an important structural change in this tropical forest, which has potentially serious implications for tree community composition and forest carbon dynamics.

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