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Increasing liana abundance and biomass in tropical forests: emerging patterns and putative mechanisms

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Abstract

Tropical forests are experiencing large-scale structural changes, the most apparent of which may be the increase in liana (woody vine) abundance and biomass. Lianas permeate most lowland tropical forests, where they can have a huge effect on tree diversity, recruitment, growth and survival, which, in turn, can alter tree community composition, carbon storage and carbon, nutrient and water fluxes. Consequently, increasing liana abundance and biomass have potentially profound ramifications for tropical forest composition and functioning. Currently, eight studies support the pattern of increasing liana abundance and biomass in American tropical and subtropical forests, whereas two studies, both from Africa, do not. The putative mechanisms to explain

increasing lianas include increasing evapotranspirative demand, increasing forest disturbance and turnover, changes in land use and fragmentation and elevated atmospheric CO_2. Each of these mechanisms probably contributes to the observed patterns of increasing liana abundance and biomass, and the mechanisms are likely to be interrelated and synergistic. To determine whether liana increases are occurring throughout the tropics and to determine the mechanisms responsible for the observed patterns, a widespread network of large-scale, long-term monitoring plots combined with observational and manipulative studies that more directly investigate the putative mechanisms are essential.

Introduction

Tropical forests contain more than half of the earth's terrestrial species and contribute more than a third of global terrestrial carbon stocks as well as nearly a third of terrestrial net primary productivity (**Dixon *et al.* 1994**; **Field *et al.* 1998**; **Wright 2010**). Thus, any alteration to tropical forests has important potential ramifications for species diversity, productivity and the global carbon cycle. Recent evidence suggests that major restructuring of tropical forests is now occurring – notably as the result of increases in forest fragmentation, logging, hunting, temperature, the intensity and duration of seasonal drought, atmospheric CO_2 and forest productivity (reviewed by **Malhi & Wright 2005**; **Wright 2005, 2010**; **Laurance *et al.*2009**).

One of the most prominent structural changes now occurring in tropical forests is the increase in liana abundance and biomass. Lianas (woody vines) are non-self-supporting structural parasites that use the architecture of trees to ascend to the forest canopy (**Schnitzer & Bongers 2002**). They are particularly abundant and diverse in lowland tropical forests, where they constitute up to 40% of the woody stems and more than 25% of the woody species, and where they can contribute substantially to forest leaf area and biomass (e.g. **Gerwing & Farias 2000**; **Chave *et al.* 2001**). Lianas typically have a high canopy to stem ratio, which allows them to deploy a large canopy of leaves above those of the host tree, thus competing aggressively with their hosts. Intense competition from lianas for both above and below-ground resources substantially limits tree recruitment, growth, diversity, reproduction and survival (reviewed by **Schnitzer & Bongers 2002**; **Paul & Yavitt 2010**; **Schnitzer & Carson 2010**), which has enormous consequences for tropical forest richness and community composition, as well as such ecosystem level dynamics as carbon, nutrient and water sequestration and fluxes (see section **Potential Ramifications of Higher Liana Abundance and Biomass** below). Therefore, the increase in liana abundance and biomass has potentially serious ramifications for tropical forest dynamics and functioning.

In this review, we synthesize the available data to conclude that lianas are increasing in abundance and biomass in American tropical and subtropical forests (section **Evidence for Increasing Liana Abundance and Biomass**). In section **Putative Mechanisms for Increasing Liana Abundance and Biomass**, we introduce the most likely mechanisms responsible for liana increases and the available empirical data supporting each mechanism. In section **Potential Ramifications of Higher Liana Abundance and Biomass**, we synthesize published evidence to demonstrate unequivocally that lianas substantially influence tropical forest community and ecosystem dynamics, supporting the argument that increases in liana abundance and biomass pose a serious threat to tropical forest dynamics and functioning. In the final section, we summarize our findings and outline future studies to determine the drivers of increasing liana abundance and biomass in tropical forests.

Evidence for Increasing Liana Abundance and Biomass

The seminal study of **Phillips *et al.* (2002a)** first documented the pattern of increasing liana abundance and biomass in tropical forests. Phillips and colleagues examined lianas ≥ 10 cm diameter in forty-seven 1-ha forest plots and lianas ≥ 2.5 cm diameter in fifty-eight 0.1-ha plots over a 2-decade period (1979–2002) in Amazonia, Northwest South America, and Central America and reported that liana abundance relative to trees increased significantly. Large lianas (≥ 10 cm diameter) had increased in basal area as much as 4.6% per year and nearly doubled in abundance over the 20-year period, while smaller lianas (≥ 2.5 cm diameter) also increased significantly, with the fastest increase occurring in the last decade of the study, thus projecting rapid future increases in liana abundance and biomass. Phillips's dataset was compelling because of the large geographical range and temporal scale examined, which indicated that rapid and large-scale changes in tropical forests were occurring.

While the size and scope of the study by Phillips and colleagues were impressive, the study was met with some initial scepticism (e.g. **Wright 2005**). One criticism was that the authors biased their study by initially selecting plots in areas that were largely free of disturbance (but see **Phillips *et al.* 2002b**). Liana abundance, diversity and biomass are substantially higher in disturbed areas, such as in treefall gaps, than in undisturbed closed-canopy forest (e.g. **Putz 1984**; **Schnitzer *et al.* 2000, 2004**; **Schnitzer & Carson 2001, 2010**). If the authors had selected sites that were free of disturbance, the initial censuses could have been biased towards finding fewer lianas. Treefalls and large branchfalls, however, occur frequently in tropical forests, with *c.* 1–2% of the forest in a disturbed state at any given time (e.g. **van der Meer & Bongers 2001**). Any undisturbed site has a high likelihood of becoming disturbed over a 20-year period, which would result in higher liana abundance, diversity, and biomass from lianas recruiting in as seedlings or, more importantly, falling from the canopy and re-rooting in the newly disturbed understory (**Putz 1984**; **Schnitzer *et al.* 2000**). Indeed, the legacy of dense liana tangles following disturbance can last decades (e.g. **Schnitzer *et al.*2000**; **Foster *et al.* 2008**; Fig. 1); thus, any disturbance in Phillips's and colleagues' study plots within the 20-year study period may have resulted in higher liana abundance and biomass.

Figure 1
Liana tangle in the forest understory on Barro Colorado Island, Panama. Liana tangles are created by treefalls, when the lianas are dragged into the treefall gap, but stay alive and eventually climb back to the forest canopy, leaving the legacy of twisted and winding stems in the forest understory. Liana tangles such as this can persist in the forest for decades (**Schnitzer *et al.* 2000**). Photo by S. Schnitzer.

In the 8 years following the publication of the study by **Phillips *et al.* (2002a)**, nearly a dozen studies using a variety of metrics have supported the pattern of increasing liana abundance, biomass, or productivity, and proposed several putative mechanisms to explain this pattern (**Benítez-Malvido & Martínez-Ramos 2003**; **Hättenschwiler & Körner 2003**; **Wright *et al.* 2004**; **Dierschke 2005**; **Schnitzer 2005**; **Körner 2006**; **Mohan *et al.* 2006**; **Wright & Calderon 2006**, **Zotz *et al.* 2006**; **Allen *et al.* 2007**; **Swaine & Grace 2007**; **Chave *et al.* 2008**; **Foster *et al.* 2008**; **Cai *et al.* 2009**; **Zhu & Cao 2009**; **Ewango 2010**; **Ingwell *et al.* 2010**; **Rutishauser 2011**). For example, in the seasonal tropical moist forest on Barro Colorado Island, Panama (BCI), **Ingwell *et al.* (2010)** found that the proportion of liana infestation in the crowns of trees changed from 32% in 1967–1968 to 47% in 1979, to nearly 75% in 2007, and the number of trees with severe liana infestation (> 75% of their canopy covered by lianas) increased 65% from 1996 to 2007. In this same forest, liana leaf litter and flower production (relative to trees) increased substantially from 1986 until 2002 (**Wright *et al.*2004**; **Wright & Calderon 2006**). Combined, these datasets provide compelling evidence that lianas are increasing on BCI.

The relative abundance and biomass of lianas also have increased in other neotropical forests (Appendix S1). In an old-growth forest at Nouragues Biological Research Station in French Guiana, **Chave *et al.* (2008)** reported that during a 10-year period from 1992 to 2002, liana abundance increased 1.8%, while tree abundance decreased 4.6%. Both liana and tree biomass increased during this period, but liana biomass increased 60% faster (lianas: 4.8% vs. trees: 3.0%). In a seasonal non-fragmented forest in central Amazon, **Benítez-Malvido & Martínez-Ramos (2003)** reported that over a 6-year period (1993–1999), recruitment of liana seedlings was 500% higher than pre-census densities, whereas tree and palm/herb seedling recruitment decreased significantly. Liana seedling recruitment also increased in 100 ha and 10 ha forest fragments over this same time period, but did not change significantly in 1-ha forest fragments, whereas tree and palm/herb recruitment decreased in all sized forest fragments (**Benítez-Malvido & Martínez-Ramos 2003**). In a strongly seasonal forest in the Bolivian Amazon, **Foster *et al.* (2008)** reported that over a 14-year period (1986–2000), low-stature liana-dense areas were persistent and increased in size across the landscape by nearly 60% (from 1.64 to 2.61 ha). In a wet aseasonal forest at La Selva Biological Station in Costa Rica, **Rutishauser (2011)** found a 20% increase in mean liana basal area and a 14% increase in liana abundance in six old-growth plots over an 8-year period from 1999 to 2007, whereas liana density in secondary forest plots did not increase over this same period. **Allen *et al.* (2007)** reported that in a sub-tropical floodplain forest in South Carolina, USA, absolute liana stem density and basal area as well as relative liana stem density (compared to trees) increased significantly over a 22-year period (1979–2001). These authors also examined a coastal floodplain forest in South Carolina and found that liana stem density and basal area increased faster than that of trees from 1990–2002 following disturbance in 1989 by Hurricane Hugo, where 20% of the trees > 10 cm diameter were killed.

Not all studies, however, have unequivocally supported the increasing liana hypothesis. **Caballé & Martin (2001)** reported that over a 13-year period (1979–1992) in a Gabonese tropical forest, the density of lianas and trees (≥ 5 cm d.b.h.) decreased 20 and 5%, respectively, whereas liana basal area remained the same while tree basal area increased slightly. In the Democratic Republic of Congo, **Ewango (2010)** found that the density of a single, highly dominant liana species in two 10-ha plots decreased 97% over a 13-year period (from 1994 to 2007), resulting in an overall decrease in liana abundance from 750 to 499 per ha (for individuals ≥2 cm d.b.h.). When excluding this one species, however, liana density remained unchanged over the 13-year period. The two African studies are particularly important because they are inconsistent with the emerging pattern of liana increases in the Americas. If this contrary pattern is ultimately confirmed by additional long-term datasets from other African forests, then researchers can test whether differences in climate, plant phylogenetic composition and relative abundance, and natural and anthropogenic disturbance vary systematically among continents and drive liana abundance, distribution and change over time.

For temperate forests, the limited data are mixed. In Germany, *Hedera helix* (English ivy) increased dramatically in abundance and range over a 24-year period (1980–2004) and has changed from a creeping plant restricted to the understory to a climbing plant found growing on many canopy trees (**Dierschke 2005**). In contrast, in 14 temperate forests in Wisconsin (USA), **Londré & Schnitzer (2006)** found that over a 45-year period (1960–2005) cumulative liana abundance and basal area had not changed, even though species population sizes had fluctuated (see also **Schnitzer *et al.* 2008a**). Likewise, in an extensive survey of 94 upland forest stands in southern Wisconsin (USA) from 1950 to 2004, **Rogers *et al.* (2008)** reported that the understory liana community abundance remained constant over time, although there was substantial variation at the species level. In 50-year-old secondary forests in the Piedmont region of New Jersey (USA), lianas were abundant and two species in particular (*Vitis* spp. and the invasive species *Celastrus orbiculatus*) were increasing in canopy cover (**Ladwig & Meiners 2010a,b**). However, it was not clear whether this increase was the result of a general increase in liana abundance or biomass in this temperate forest, or of a natural succession sequence.

Invasive lianas in particular are predicted to increase in abundance and biomass in temperate and subtropical forests, especially after natural or anthropogenic disturbance (e.g. **Gallagher *et al.* 2010**). In North America, there are more than 80 non-native liana species (**Londré & Schnitzer 2006**), including kudzu (*Pueraria lobata*), oriental bittersweet (*C. orbiculatus*), English ivy (*H. helix*) and Japanese honeysuckle (*Lonicera japonica*). These invasive lianas can proliferate rapidly and substantially alter forest community composition and dynamics (**Sasek & Strain 1991**; **Gallagher *et al.* 2010**). For example, oriental bittersweet is now expanding in North American forests, where it can reduce native tree regeneration and survival (**Fike & Niering 1999**). Following hurricane damage in a Florida (USA) hardwood forest, invasive lianas rapidly colonized the damaged forest and persisted for many years afterwards, substantially reducing native tree, shrub and herb regeneration (**Horvitz & Koop 2001**). Native lianas may also experience more vigorous growth and range expansion in response to CO_2 (e.g. **Mohan *et al.* 2006**; **Zotz *et al.* 2006**) and forest fragmentation (e.g. **Londré & Schnitzer 2006**). One of the major factors limiting liana abundance in temperate forests is freezing temperature (**Sperry *et al.* 1987**; **Schnitzer 2005**) and thus both native and exotic lianas are likely to increase most rapidly in forests that do not experience long cold winters.

Putative Mechanisms for Increasing Liana Abundance and Biomass

Empirical evidence supporting the putative mechanisms to explain liana increases is typically correlative due to the difficulty in conducting long-term, large-scale multi-forest manipulations over the appropriate time periods. Nonetheless, correlative data combined with sound theoretical expectations provide insight into mechanistic explanations for observed patterns. These insights can then be tested experimentally. Below we describe four putative mechanisms to explain increasing liana abundance and biomass and the available data to support or refute them.

Increased evapotranspirative demand

Increasing evapotranspirative demand may drive liana changes because liana abundance, biomass and relative species richness increase with decreasing rainfall and increasing seasonality and temperature (i.e. increased evapotranspirative demand; Fig. 2; **Schnitzer 2005**; **Swaine & Grace 2007**; **DeWalt *et al.* 2010**). **Schnitzer (2005)** posited that lianas have a dry season growth advantage due to their ability to access and efficiently use soil water during seasonal drought, which allows them to grow when many of their competitors, such as trees, are dormant. In addition, strong stomatal control may allow lianas to limit water loss, which could enable them to grow during seasonal drought (e.g. **Cai *et al.* 2009**). Growth during the dry season is particularly advantageous because light, which is typically limiting in tropical forests, is far more abundant during the dry season because of decreased cloud cover and lower canopy density due to the large number of deciduous trees (e.g. **Condit *et al.* 2000**; **Graham *et al.* 2003**). The dry season growth advantage of lianas could result in their relatively high abundance in seasonal forests. In contrast, lianas may lack this advantage in aseasonal wet forests, where they are less abundant, because soil moisture is rarely limiting and the understory is dark due to year-round cloud cover and dense forest canopies (**Schnitzer 2005**).

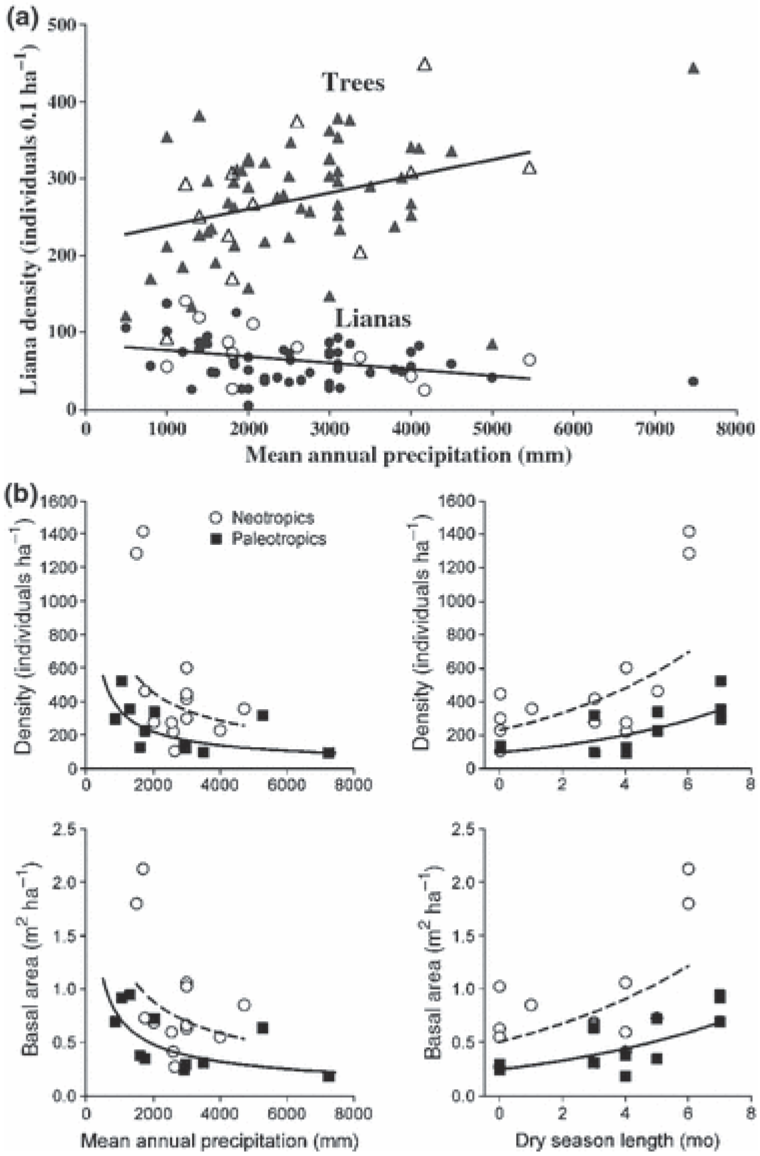

Figure 2

(a) The density of lianas (circles) and trees (triangles) (≥ 2.5 cm) in 66 tropical lowland forests from Africa (8), Asia (4), C. America (9), and S. America (45) regressed over mean annual precipitation (from **Schnitzer 2005**). Lianas decreased significantly ($P = 0.01$, $r^2 = 0.10$, $n = 66$), whereas trees increased marginally ($P = 0.097$, $r^2 = 0.10$, $n = 66$). Closed symbols represent neotropical, open = paleotropical sites. (b) The density and basal area of lianas (≥ 2.5 cm) in neotropical (solid line) and paleotropical forests (dashed line) regressed over mean annual rainfall and dry season length (from **DeWalt *et al.* 2010**). Both liana density and basal area decreased with increasing rainfall and increased with the length of season drought.

Evidence that lianas have the capacity to grow during seasonal droughts when evapotranspirative demand is high is derived from both growth and physiology measurements, as well as from phenological studies. For example, **Schnitzer (2005)** found that lianas in a Panamanian forest grew two times faster than trees during the wet season and seven times faster during the dry season, suggesting that lianas capitalized on dry season resources and suffered substantially less water stress than did trees. Likewise, **Cai *et al.* (2009)** reported that lianas in a seasonal tropical forest in southwestern China fixed carbon and used water more efficiently than trees, particularly during the dry season, a finding which supports the dry season growth advantage hypothesis. Also in southwestern China, **Zhu & Cao (2009)** found that lianas had higher hydraulic conductivity, maximum carbon assimilation rate and pre-dawn leaf water potential than trees during the dry season. In Ghana, **Swaine & Grace (2007)** reported that drier forests had a 43% higher proportion of liana species than did wetter forests (43 vs. 30%), suggesting that liana species are adapted to habitats with high evapotranspirative demand.

The ability of lianas to remain evergreen during the dry season may also confer a dry season growth advantage. On BCI, Panama, nearly all of the lianas remain evergreen throughout the year, whereas approximately 30% of the tree species lose their leaves at some point during the dry season (**Putz & Windsor 1987**; **Condit *et al.* 2000**). **Putz & Windsor (1987)** reported that > 90% of 43 liana species examined on BCI actually produced new leaves during the dry season, a process requiring an ample supply of water, whereas < 50% of the 26 tree species examined produced new leaves. In a dry forest in the Guanacaste Province in Costa Rica with a severe and extended dry season, **Kalácska *et al.* (2005)** found that lianas retained their leaves and became deciduous only at the very end of the dry season, far later than most trees. In the same forest, **Opler *et al.* (1991)** found lianas to produce new leaves late in the dry season, presumably when water was most scarce. Collectively, these studies indicate that lianas are favoured in seasonal forests with high evapotranspirative demand.

Evapotranspirative demand is increasing in tropical forests and may explain the increase in liana abundance and biomass relative to competing trees. Throughout the tropics, temperature and severity of seasonal drought have increased, rainfall has decreased (**Malhi & Wright 2005**) and future increases in the occurrence and severity of drought are predicted (e.g. **Phillips *et al.* 2009**; **Lee & McPhaden 2010**). Currently, the increase in temperature has only minor variation among regions, whereas changes in rainfall and dry season intensity are far more variable among and within regions and thus may be more site-specific (**Malhi & Wright 2005**; **Asner & Alencar 2010**). For example, Amazonian forests are experiencing decreasing precipitation, especially during seasonal droughts (**Phillips *et al.* 2009**), which benefits lianas and may explain their documented increases. In Panama, where **Ingwell *et al.*(2010)** and Wright and colleagues (**Wright *et al.* 2004**; **Wright & Calderon 2006**) found profound increases in liana infestation and productivity, annual precipitation decreased nearly 20% during 60 years (1930–1990). Although rainfall in the 1990s returned to the levels of 1930s, the 60 years of declining rainfall may have ameliorated the environment for liana establishment and proliferation (**Schnitzer 2005**). Many forests throughout the tropics are projected to suffer water stress from increasing frequency and intensity of ENSO-related droughts (e.g. **Lee & McPhaden 2010**), which would increase liana abundance and biomass.

If tropical forests experience extreme multi-year droughts that deplete even deep-water sources, such as the 4-year drought experimentally imposed in a forest in Tapajós, Brazil, lianas would probably suffer considerably (**Nepstad *et al.* 2007**). Under this scenario, the efficient vascular system of lianas, which is beneficial when some soil water is present, would make them particularly vulnerable to embolism when deep soil water is scarce, which would increase mortality and ultimately decrease liana abundance and biomass. Evergreen trees would also suffer much higher mortality, and tropical forests would shift to being dominated by deciduous trees (**Nepstad *et al.* 2007**). Nonetheless, the current rate of increasing evapotranspirative demand in many tropical forests is likely to favour liana proliferation.

Increasing rates of natural disturbance

There is now overwhelming evidence that liana abundance, biomass and diversity increases with disturbance, tree mortality and forest turnover (e.g. **Putz 1984**, **DeWalt *et al.* 2000**, **Schnitzer *et al.* 2000, 2004, 2008b**; **Schnitzer & Carson 2001, 2010**). Lianas capitalize on disturbed areas because they first recruit into them with large numbers and then grow rapidly in the high-resource environment. Lianas may be particularly abundant and diverse in such disturbed areas as treefall gaps because they can colonize gaps by seed, advance regeneration, lateral growth from the intact understory along the forest floor (e.g. **Peñalosa 1984**; **Schnitzer *et al.* 2000**), and long-distance clonal recruitment (**Rutishauser 2011**), whereas trees typically use only the first two methods (**Schnitzer *et al.* 2000, 2008b**). Lianas commonly fall into understory following a canopy disturbance (**Putz 1984**; **Schnitzer *et al.*2000**; **Phillips *et al.* 2005**; **Ingwell *et al.* 2010**), where adult stems re-root and produce new stems (**Fig. 3**). As many as 90% of the lianas pulled into a gap during the treefall can survive and regenerate in the gap (**Putz 1984**).

Figure 3

Lianas covering a recent fallen tree on Barro Colorado Island, Panama. Nearly all of the leaves in the foreground belong to the liana *Coccoloba parimensis*(Polygonaceae), one of the most common liana species on Barro Colorado Island and one with a high propensity for vegetative reproduction (S. Schnitzer, unpublished data). Photo by S. Schnitzer.

Lianas can also recruit into the forest as adults from minor canopy disturbance. At La Selva Biological Station, **Rutishauser (2011)** found that long-distance clonal recruitment of lianas that fell into the understory after minor canopy disturbance (e.g. small treefalls and branchfalls) contributed 7.5% to the increase in lianas abundance and 60% to the increase in liana biomass over an 8-year period (from 1999 to 2007). Upon arrival in a gap, liana growth rate and vegetative stem production far exceed those of trees, probably because lianas allocate only a fraction of carbon to support tissue, which allows them to proliferate and grow rapidly in the high-resource environment of a gap; thus enabling them to eventually climb successfully back to the forest canopy (**Putz 1984**; **Schnitzer *et al.* 2000, 2004**). The ability of lianas to regenerate in gaps does not mean that lianas are shade-intolerant; in fact, they appear to vary in shade-tolerance as much as trees (**Gilbert *et al.* 2006**). Instead, many lianas are shade-tolerant and can capitalize on disturbance through rapid growth, which may give them the appearance of being shade-intolerant, thereby leading to confusion about their ability to tolerate shaded conditions.

Rates of canopy tree mortality and forest turnover may be increasing in many tropical forests because of elevated temperature, atmospheric CO_2 concentration and nutrient deposition (**Phillips & Gentry 1994**; **Phillips *et al.* 2005**, **Wright 2010**). Increased temperature raises nighttime respiration rates and may reduce tree growth and increase mortality (**Clark 2004**). Alternatively, increased nutrient deposition and atmospheric CO_2 concentrations could increase forest productivity, causing canopy trees to grow faster and thus die faster (**Phillips & Gentry 1994**; **Phillips *et al.* 2005**; **Körner 2006**). Similarly, an increase in the intensity and length of droughts, including severe El Nino events (Zhang *et al.* 2007, **Li *et al.*2008**, **Phillips *et al.* 2009**) leads to increased forest turnover and treefall gap formation (**Slik 2004**; **Wright 2005**), and thus an increase in liana abundance and biomass (**Putz 1984**; **Schnitzer *et al.* 2000, 2008b**; **Schnitzer & Carson 2001**).

Lianas themselves may be partially responsible for increasing forest turnover and gap formation, and therefore lianas may be increasing their own abundance and biomass through positive feedback. Liana removal experiments have demonstrated that lianas can severely reduce tree growth (e.g. **Grauel & Putz 2004**; **Schnitzer & Carson 2010**; Tobin, M., Wright, A., Mangan, S. & Schnitzer, S.A., unpublished data), which, in turn, could lead to higher tree mortality and thus increase the rate of gap formation. Indeed, **Ingwell *et al.*(2010)** found that trees that are heavily infested by lianas had twice the probability of mortality as trees with lesser amounts of liana infestation. Consequently, the increase in lianas may slow tree growth and increase tree mortality, thus increasing gap formation and forest turnover and leading to a positive feedback cycle of increasing liana abundance and biomass.

Changing land-use

Anthropogenic disturbance of tropical forests, such as logging, forest fragmentation and hunting, may also be contributing to increases in liana abundance and biomass. Logging, even at very low and sustainable levels that are common in many forests (≥1 canopy tree ha^{-1}; **Parren & Doumbia 2005**; **Asner *et al.* 2006**) could increase liana abundance and biomass because of the newly created treefall gaps, as well as the collateral disturbance associated with tree extraction (**Addo-Fordjour *et al.* 2009**). High rates of deforestation in the tropics are a global problem (e.g. **Wright 2005, 2010**; **Laurance *et al.* 2009**) and even wide expanses of forest previously classified as old-growth are now thought to be affected by selected logging (**Asner *et al.* 2006**). These anthropogenic disturbances, even at relative low intensities, increase liana abundance and biomass because of the propensity of lianas to capitalize on disturbance.

In contrast to tropical forest destruction, secondary forest creation may also be driving an increase in liana abundance. In many tropical areas, young secondary tropical forests are expanding in size and frequency as more people abandon marginally productive farmland for more lucrative work in urban areas (**Chazdon 2003**; **Wright 2005, 2010**). Thus, while old-growth forests continue to be lost, total forested area may be increasing because of the regeneration of secondary forests (**Wright 2005, 2010**). These young secondary forests have a much greater proportion of lianas than older forests have. For example, in studies of tropical forest succession, liana stem density (both absolute and relative to trees) peaks in young secondary forests (≥ 40 years old), and decreases as the forest ages (**DeWalt *et al.*2000**, **Letcher & Chazdon 2009**). Secondary forests may provide ideal conditions for liana proliferation by providing an optimal balance of trellises and high light (**Madeira *et al.* 2009**), and thus the increase in secondary forest area will be accompanied by higher liana abundance.

Forest fragmentation will also result in higher liana abundance and biomass. Lianas regenerate aggressively on forest edges, where they can take advantage of the drier conditions and higher light to climb into and drape over the canopy. For example, **Laurance *et al.* (2001)** reported that liana abundance and biomass increased significantly in the high light and more arid conditions of tropical forest edges compared with intact forest (see also **Arroyo-Rodriguez & Toledo-Aceves 2009**). **Londré & Schnitzer (2006)** found a similar phenomenon in temperate hardwood forests, with lianas peaking in abundance very close to the edge and tapering off rapidly with distance from the edge into the forest. With the creation of new roads, clear-cutting, power lines and other forms of forest fragmentation (**Laurance *et al.* 2009**), the increase in forest edges will result in higher liana abundance. Furthermore, higher liana abundance in fragmented and secondary forests will result in more liana propagules and may enhance liana regeneration in nearby old-growth forests – even ones that are not obviously impacted by humans.

Hunting and the bush-meat trade may have a cascading effect on plant species composition by eliminating seed predators and dispersers, which may increase liana abundance (**Wright *et al.* 2007**). Hunting is rampant in tropical forests, dramatically reducing the mammal and bird communities that serve as important seed predators and dispersers (e.g. **Wright *et al.*2007**). The reduction in seed predators will favour large seeded species, which tend to be eaten preferentially because of their high nutrient content, as well as wind-dispersed species, which do not need specialized seed dispersers. As a larger proportion of lianas are wind dispersed compared to trees (**Gentry 1991**), liana regeneration is predicted to increase in forests where hunting is common. Indeed, **Wright *et al.* (2007)** showed that seedlings of liana species were significantly more abundant in forests with hunting than in forests that lacked hunters, and that wind-dispersed liana species was responsible for this trend. Thus, hunting, in combination with other land-use changes such as logging and forest fragmentation, may contribute to increases in liana abundance and biomass in tropical forests.

Elevated atmospheric CO_2

Lianas grow rapidly under elevated CO_2 concentrations (**Granados & Korner 2002**; **Belote *et al.* 2003**; **Hättenschwiler & Körner 2003**, **Mohan *et al.* 2006**; **Zotz *et al.* 2006**), and thus increasing atmospheric CO_2 has been proposed to explain corresponding increases in lianas (e.g. **Phillips *et al.* 2002a**). While studies comparing tropical lianas with trees in ambient and elevated CO_2 conditions are lacking, temperate lianas have been found to respond faster than trees to elevated CO_2 concentrations (**Belote *et al.* 2003**; **Hättenschwiler & Körner 2003**). Temperate lianas such as poison ivy (*Toxicodendron radicans*) responded strongly to elevated CO_2, and consequently poison ivy may become more abundant and also more toxic in temperate forests (**Mohan *et al.* 2006**; but see **Schnitzer *et al.* 2008a**). The most abundant western European liana, English ivy (*H. helix*) benefitted strongly from increased CO_2, particularly in the forest understory (**Zotz *et al.* 2006**) – a response that presumably allows *Hedera* to vigorously explore light-limited understory microhabitats and increases the likelihood of its reaching the forest canopy (e.g. **Dierschke 2005**).

One theoretical explanation for the reason that lianas respond more than trees to elevated CO_2 is based on the relatively high ratio of leaf area to total plant mass (LAR) of lianas (e.g. **Cai *et al.* 2009**; **Zhu & Cao 2009, 2010**). The leaf area ratio hypothesis posits that if lianas and trees have similar photosynthetic capacity per unit leaf area, then lianas would grow proportionately faster under elevated CO_2 conditions because the greater leaf area will allow lianas to fix more carbon per total plant biomass. This positive feedback would accelerate as the higher LAR allows lianas to add more photosynthetic tissue per unit biomass gain compared with trees, thus enabling them to fix even more carbon. Furthermore, liana leaf characteristics may allow them to utilize elevated atmospheric CO_2more efficiently than trees. **Zhu & Cao (2010)** showed that compared with trees, liana leaves had consistently higher specific leaf area and photosynthetic rates, high photosynthetic nitrogen and phosphorus use efficiencies, and lower leaf construction costs and leaf life span – attributes that should lead to a faster response to atmospheric CO_2 enrichment (see also **Cai *et al.* 2009**).

Higher concentrations of atmospheric CO_2 also may allow plants to use water more efficiently because they are able to uptake more carbon per unit time that their stomata are open, thus allowing them to fix more carbon per unit water loss through transpiration. This dynamic is particularly important in seasonal forests, the most common forest type in the tropics, where both lianas and trees become water-stressed during the dry season (**Schnitzer 2005**). As lianas are better adapted to grow under drought conditions than trees (**Schnitzer 2005**; **Domingues *et al.* 2007**; **Cai *et al.* 2009**; **Zhu & Cao 2009**), lianas are more likely to take advantage of the additional carbon gained per unit water loss under a high CO_2environment. Higher CO_2 also should increase tree carbon fixation, but possibly not as much as for lianas because many trees may still be too water-stressed during seasonal drought to take advantage of the benefits of elevated atmospheric CO_2. In addition, many tree species are adapted to avoid drought by dropping leaves, thus limiting physiological activity during the dry season. While both the LAR and water-use hypotheses are theoretically possible, there is currently little empirical evidence directly linking either mechanism to observed increases in liana abundance or biomass.

Potential Ramifications of Higher Liana Abundance and Biomass

Lianas play an important role in tropical forest dynamics, and the increase in lianas may substantially alter tropical forest community composition and ecosystem level dynamics. At the community level, both experimental and observational studies confirm that lianas substantially decrease tree diversity, recruitment, growth, fecundity and survival in both the intact forest and in treefall gaps (**Schnitzer *et al.* 2000**; **Grauel & Putz 2004**; **Schnitzer 2005**; **Wright *et al.* 2005**; **Toledo-Aceves & Swaine 2007, 2008a,b**; **van der Heijden *et al.* 2008**; **Peña-Claros *et al.* 2008**; **Ingwell *et al.* 2010**). For example, in an 8 year liana removal experiment, **Schnitzer & Carson (2010)** found that lianas limited recruitment, growth and diversity of trees regenerating in treefall gaps. Tightly controlled experimental studies testing the competitive effects of lianas on tree seedlings and saplings also demonstrate that lianas compete intensely with trees, particularly for belowground resources (**Schnitzer *et al.*2005**, **Chen *et al.* 2008**; **Toledo-Aceves & Swaine 2008a**).

Lianas do not affect all trees equally, and thus they may be a determinant of tree species coexistence by competing intensely with some tree species, but not with others. Lianas have a particularly strong effect on the growth and survival of slower-growing shade-tolerant trees (**Putz 1984**; **van der Heijden *et al.* 2008**; **Peña-Claros *et al.* 2008**; **Ingwell *et al.* 2010**; **Schnitzer & Carson 2010**). In contrast, pioneer trees seem to be impervious to the presence of lianas and grow equally well regardless of nearby liana abundance (e.g. **Putz 1984**; **Schnitzer *et al.* 2000**; **Toledo-Aceves & Swaine 2007**; **Schnitzer & Carson 2010**).

Extending the findings of liana removal experiments to predicting forest-wide effects of increasing liana abundance and biomass requires caution because the removal of any vegetation should result in the growth of the remaining plants. Liana removal studies demonstrate that lianas compete intensely with trees, but these studies cannot test whether these effects are unique to lianas. This is an important consideration because if lianas increase in relative biomass at the expense of trees, and both lianas and trees compete equally, then there may be no net change in forest-wide competitive effects from an increase in lianas. We tested the uniqueness of liana competition by cutting an equal amount of biomass of either lianas or trees rooted underneath the crowns of target trees (Tobin *et al.*, unpublished data). We found that cutting lianas resulted in an immediate increase in target tree sap-flow – a proxy for photosynthesis and carbon fixation – whereas cutting the same biomass of trees did not alter target tree sap flow. Lianas likely have a uniquely strong competitive effect on canopy trees because even relatively small lianas (≥ 2.5 cm diameter) consistently reach the forest canopy (**Kurzel *et al.* 2006**), where they deploy their leaves above those of the host tree and thus compete for both aboveground and belowground resources. In contrast, similar-sized trees are trapped in the understory, where they consume relatively few resources (Tobin *et al.*, unpublished data).

At the ecosystem level, lianas may have a large effect on carbon, nutrient and water dynamics by decreasing whole-forest carbon sequestration and storage, redistributing nutrients horizontally across the forest landscape and reducing available soil moisture during seasonal droughts (**Schnitzer *et al.* 2000, 2006**; **Powers *et al.* 2004**; **Andrade *et al.*2005**; **Schnitzer 2005**). Lianas, more than any other growth form, appear to have a disproportionately large impact on carbon dynamics in relation to their stand-level aboveground biomass (AGBM). Liana stems generally contribute less than 10% of the AGBM in mature tropical forests (**Putz 1983**, **DeWalt & Chave 2004**), but they can contribute as much as 30% of the AGBM in liana-dense areas (**Gerwing & Farias 2000**). However, as liana abundance and biomass increase, forest-wide biomass can decrease because heavy liana infestations increase tree mortality and reduce tree growth (e.g. **van der Heijden & Phillips 2009**; **Ingwell *et al.* 2010**; **Schnitzer & Carson 2010**), which reduces the total amount of carbon sequestered in tree biomass (**Körner 2006**). For example, in liana-dense areas of a forest in French Guiana, tree AGBM was around one-third lower than the mean tree AGBM of the entire forest (**Chave *et al.* 2001**). The loss in tree AGBM was not offset by the increase of liana AGBM because lianas have relatively slender stems and low wood volume and thus they sequester far less carbon than do trees (**Laurance *et al.* 1997**; **Chave *et al.* 2001**; **Schnitzer *et al.* 2006**). **Van der Heijden & Phillips (2009)** reported that lianas reduced tree AGBM increment by 10% annually in the Peruvian Amazon, whereas the AGBM increment of lianas compensated only around 30% of this loss. In central Amazonia, tree abundance decreased and liana abundance increased within 100 m of the forest edge 10–17 years following forest fragmentation; however, tree AGBM decreased substantially by 36.1 Mg ha^{-1}, while liana AGBM increased only slightly (0.46 Mg ha^{-1}; **Laurance *et al.* 1997, 2001**). Lianas may further alter forest carbon pools and fluxes by having a strong inhibitory effect on the growth and regeneration of shade-tolerant tree species with high wood density, but not on light-wooded pioneer trees (e.g. **van der Heijden & Phillips 2009**; **Schnitzer & Carson 2010**). Consequently, the impact of lianas on whole-forest AGBM may be substantial, and far greater than predictions based on their relatively limited direct contribution to forest biomass.

Lianas may alter soil nutrient dynamics and redistribute nutrients within forests. Tree species differ greatly in leaf-nutrient levels and chemical composition, and thus they are expected to produce unique species–specific signatures in the soil beneath their crowns (e.g. **Powers *et al.* 2004**, **Hättenschwiler *et al.* 2008**). **Powers *et al.* (2004)** reported a lack of tree-specific soil signatures at La Selva Biological Station in Costa Rica and proposed that lianas may have obscured the expected signatures by homogenizing leaf litter deposition. Compared with tropical trees, tropical liana leaves often have high foliar nitrogen (**Kusumoto & Enoki 2008**) and phosphorus content (**Cai & Bongers 2007**), and thus high liana densities may alter soil nutrient levels. However, liana crowns can extend hundreds of metres away from their root system (**Putz 1984**), allowing them to acquire soil nutrients and deposit their nutrient-rich litter far from their roots, thereby potentially redistributing and homogenizing soil nutrients within forests (**Powers *et al.* 2004**).

Lianas affect whole-forest water dynamics by altering forest structure and maintaining high transpiration rates during seasonal droughts. Lianas change forest structure by stalling tree regeneration in treefall gaps for decades (**Schnitzer *et al.* 2000**; **Foster *et al.* 2008**). Increased solar radiation, decreased humidity and the capacious ability of lianas to uptake water from the soil result in liana-dominated gaps that become drier over time (**Foster *et al.* 2008**). Although data are limited, lianas appear to have well-developed root and vascular systems, which presumably allow them to compete effectively for belowground resources in gaps and in intact forest during seasonal droughts (**Pérez-Salicrup & Barker 2000**; **Andrade *et al.*2005**; **Schnitzer 2005, 2005**; **Toledo-Aceves & Swaine 2008a**). For example, in eastern Amazonia, even small *Davilla kunthii* (Dilleniaceae) lianas (< 1.4 m tall) had root systems exceeding 10 m in depth, and lianas with deep root systems had relatively high water potentials (**Restom & Nepstad 2001, 2004**). Furthermore, lianas transpired more than similar-sized trees, and lianas accounted for up to 12% of forest transpiration, even though all lianas combined were only 5% of the forest basal area (**Restom & Nepstad 2001, 2004**). Consequently, an increase in liana abundance, biomass and leaf area will alter water dynamics in tropical forests.

Summary and Future Directions

Over a dozen studies have evaluated long-term data to test the pattern of increasing liana abundance or biomass or both. Of these, eight are from the American tropics and subtropics, two are from the African tropics and four are from North American and European temperate forests (Appendix S1). All eight neotropical and subtropical studies provide evidence for increasing liana abundance or biomass or both, which represents a major change in neotropical forests with important ramifications for community and ecosystem dynamics. In contrast, the two African studies did not find an increase in lianas.

While additional long-term data from palaeotropical forests are necessary to confirm whether lianas are truly responding differently among the continents, comparisons at the continental scale are important because they provide insights into the mechanisms responsible for the pattern. For instance, differing changes in climate, disturbance or land-use could explain why lianas are increasing on some continents and not on others if these factors vary at the continental scale. Phylogenetic differences in liana communities among continents may be responsible for differing patterns in liana abundance and biomass if liana changes are driven by select taxa that differ among continents. For example, the most species-rich liana families in neotropical forests are the Bignoniaceae and the Fabaceae, whereas the most species-rich liana families in African forests tend to be the Apocynaceae, Connaraceae and Celastraceae (**Gentry 1991**; **Ewango 2010**). Functional trait differences among liana species may determine the taxa that are increasing and decreasing, and linking liana population changes to functional traits will provide an insight into the factors driving liana abundance and distribution.

Alternatively, the pattern of liana change may be a more local than continental phenomenon, with lianas increasing in some areas and decreasing or remaining the same in others. Lianas would not be expected to increase uniformly at the continental scale if the processes that determine liana abundance vary within this scale. For example, if the increase in the strength and duration of seasonal drought is the underlying cause of increasing liana abundance, then we should expect lianas to change the most in areas most affected by the change in rainfall regimes. Likewise, changes in disturbance and land-use may also explain liana change, and detailed data on forest-specific disturbance and rainfall regimes will allow for tests of these putative mechanisms.

The first step in refining our understanding of global patterns of liana change is to expand the collection of long-term, large-scale liana datasets in temperate and tropical forests. Additional liana datasets from Africa, Asia and Australia will be particularly important to test whether liana changes occur on the continental scale. Comprehensive long-term species-level data for multiple forests are necessary to test whether a subset of liana taxa are driving the pattern of liana change, and whether phylogenetic and functional trait differences explain liana changes among continents. A widespread network of long-term monitoring plots of lianas and trees using uniform sampling protocols (e.g. **Gerwing *et al.* 2006**, **Schnitzer *et al.* 2008b**) is essential to determine the patterns of large-scale tropical forest change. The Center for Tropical Forest Science (CTFS) model of large plots distributed worldwide provides an excellent way to monitor liana changes in tropical and temperate forests. Unfortunately, of the 40 CTFS plots in 21 countries, very few have included lianas and only a couple of plots (e.g. Ituri in Democratic Republic of Congo and BCI in Panama) have a complete 40 or 50 ha liana census (**Schnitzer *et al.* 2008b**; **Ewango 2010**).

To date, there is limited empirical evidence for the putative mechanisms responsible for liana changes. Detailed measurements of multiple liana and tree species' physiological responses to varying ambient conditions within and among forests, including water potential, leaf- and whole plant-level gas exchange, rooting depths, stomatal activity and detailed growth measurements across seasons and years are necessary to test hypotheses of how lianas and trees differ in response to changing conditions. Forest-level data on disturbance, rainfall, seasonality, temperature and atmospheric CO_2 are necessary to test for correlations between these factors and liana abundance and biomass among forests. Data on how these factors are changing are necessary to test whether they are potential drivers of lianas change within forests. We are assuming that changes in one or more abiotic factors are responsible for liana increases, an assumption that must be tested empirically.

Detailed experimentation is necessary to confirm whether liana and tree species are responding differently to the environmental factors associated with each of the putative mechanisms, and whether these factors are responsible for the observed changes in liana abundance and biomass. The potential for increasing atmospheric CO_2, evapotranspirative demand, forest turnover and disturbance and land-use changes to operate both independently and synergistically makes these experiments challenging. Nevertheless, fully factorial manipulations of atmospheric CO_2, water (evapotranspirative demand), and light (disturbance) for replicated liana and tree species across varying life-history stages will allow us to determine the factors that favour lianas over trees. Including a range of liana and tree species that vary in functional traits allows us to test whether plant functional traits predict the species that will most likely respond to each global change factor.

The underlying and pivotal mechanism responsible for liana abundance may be the physiological ability of lianas to grow during periods of water stress and high evapotranspirative demand, which would strengthen and reinforce each of the other three mechanisms. For example, liana growth during periods of water stress and high evapotranspirative demand is probably enhanced by elevated atmospheric CO_2, which increases liana growth without increasing water consumption. As lianas are able to grow much more than trees during seasonal droughts (**Schnitzer 2005**; **Cai *et al.* 2009**; **Zhu & Cao 2009**), elevated atmospheric CO_2 concentrations could allow lianas to take advantage more fully of concomitant decreases in rainfall. Likewise, elevated atmospheric CO_2 may increase forest productivity (**Phillips & Gentry 1994**; **Körner 2006**), eventually leading to increased forest turnover and disturbance, which provide an ideal environment for liana proliferation. Liana regeneration is favoured in disturbed areas because lianas are able to take advantage of the elevated resources, particularly light, despite the high evapotranspirative demands found in gaps (**Schnitzer 2005**; **Foster *et al.* 2008**). At present, data supporting the synergistic relationship among these factors data are limited; therefore, additional species–specific studies that manipulate these factors are necessary.

We can confirm the factors responsible for increasing lianas by linking (1) long-term empirical data on liana changes (relative to trees) in multiple forests, (2) empirical data on the changes in the environmental factors that are presumed to drive increasing relative liana abundance and biomass (within individual forests over time and among forests that vary in liana abundance and biomass), (3) experimental data confirming that lianas (relative to trees) respond strongly to these factors in isolation and in conjunction with each other and (4) the functional traits responsible for liana and tree responses. While the experiments outlined above may be logistically difficult, particularly for atmospheric CO_2, which is expensive, they are necessary to confirm the putative mechanisms responsible for the large-scale and important structural changes in tropical forests that we are witnessing.

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