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Stefan A. Schnitzer
Marquette University, stefan.schnitzer@marquette.edu

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Testing Ecological Theory with Lianas

Stefan A. Schnitzer
Department of Biological Sciences, Marquette University, Milwaukee, WI
Smithsonian Tropical Research Institute, Balboa, Republica de Panama

Summary

Lianas constitute a diverse polyphyletic plant group that is advancing our understanding of ecological theory. Specifically, lianas are providing new insights into the mechanisms that control plant distribution and diversity maintenance. For example, there is now evidence that a single, scalable mechanism may explain local, regional, and pan-tropical distribution of lianas, as well as the maintenance of liana species diversity. The ability to outcompete trees under dry, stressful conditions in seasonal forests provides lianas a growth advantage that, over time, results in relatively high abundance in seasonal forests and low abundance in aseasonal forests. Lianas may also gain a similar growth advantage following disturbance, thus explaining why liana density and diversity peak following disturbance at the local, forest scale. The study of ecology, however, is more than the effect of the environment on organisms; it also includes the effects of organisms on the environment. Considerable empirical evidence now indicates that lianas substantially alter their environment by consuming resources, suppressing tree performance, and influencing emergent properties of forests, such as ecosystem functioning, plant and animal diversity, and community composition. These recent studies using lianas are transcending classical tropical ecology research and are now providing novel insights into fundamental ecological theory.

I. Introduction

One of the fundamental and even definitional goals in ecology is to formulate mechanistic explanations for the abundance and distribution of organisms (e.g. Andrewartha & Birch, **1954**; Brown, **1984**). This definition of ecology incorporates both the biotic and abiotic forces that determine the diversity, composition, structure, and functioning of Earth's ecosystems. Two goals that are integral to understanding the abundance and distribution of organisms are to determine the mechanisms responsible first for the distribution of organisms across multiple spatial scales, from local to global (e.g. Brown, **1984**) and second for the maintenance of the diversity of those organisms in any given ecosystem (e.g. Tilman, **1982**). An even more ambitious goal in ecology is to formulate and test a single unifying mechanistic theory for both the distribution of organisms and the maintenance of diversity across multiple spatial scales (*sensu* Whittaker *et al*., **2001**).

Most tests of ecological theory to explain the distribution of organisms and the maintenance of their diversity have been, perhaps by necessity, narrowly focused. For example, in forests, particularly in tropical forests, the vast majority of the tests of theory utilized trees exclusively (e.g. Harms *et al*., **2001**; Potts *et al*., **2004**; John *et al*., **2007**; Mangan *et al*., **2010**; LaManna *et al*., **2017**). The use of trees to test theory in ecology has led to major advances in our understanding of the distribution and abundance of organisms (e.g. Johnson *et al*., **2017**; Chen *et al*., **2018**; Turner *et al*., **2018**). However, testing key ecological theory exclusively with a single growth form fails to provide a general test due to the convergent life-history characteristics within growth forms. Trees in particular tend to converge on similar traits: they are tall in stature and commonly have animal-dispersed seeds. Thus, trees may rely more on dispersal-based theories for their distribution and the maintenance of their diversity compared with short-statured or wind-dispersed plants (Barry & Schnitzer, **2016**; Clark *et al*., **2018**). Therefore, testing ecological theory solely with trees limits our understanding of the generality of these theories. Testing ecological theory with co-occurring tree and nontree plant groups is a way to redress this omission.

Lianas are an iconic, easily recognizable, abundant, and taxonomically diverse nontree component of many forest communities that are now being used to test ecological theory (Fig. **1**; Box **1**). There are three main reasons why testing ecological theory with lianas can advance the field of ecology. First, lianas provide an ideal complement and contrast to trees to test the generality of ecological theory. Both lianas and trees are diverse polyphyletic plant groups with an overlapping range of functional characteristics (e.g. Gilbert *et al*., **2006**; Asner & Martin, **2015**; Isnard & Feild, **2015**). Lianas are similar to trees taxonomically (Gianoli, 2004, **2015**), and many congeneric and confamilial liana and tree species coexist in the same forest (e.g. Schnitzer *et al*., **2012**, **2015a**). As a group, however, lianas differ from trees in key life-history strategies, which are expressed through differences in their anatomical, physiological, and chemical attributes (Zhu & Cao, **2009**, 2010; Wyka *et al*., **2013**; Angyalossy *et al*., **2015**; Asner & Martin, **2015**; Isnard & Feild, **2015**; Rowe & Speck, **2015**; Santiago *et al*., **2015**; Maréchaux *et al*., **2017**). Therefore, if the same mechanisms that maintain species diversity and control distributions apply to both lianas and trees, we are closer to formulating a general understanding of the fundamental questions in ecology. Second, lianas may be the first diverse and broadly distributed plant group for which we can formulate a scalable mechanistic explanation for both their distribution and the maintenance of their species diversity. Below, I argue that the same underlying mechanism to explain the maintenance of liana diversity at the local scale may also explain the distribution of lianas from local to regional to pantropical scales, and can even be extended to latitudinal and altitudinal scales. Thus, lianas may provide key insights into formulating a single unifying explanation for organismal distribution and diversity. Third, understanding the ecology of lianas themselves is key to understanding the ecology of most tropical and many temperate forests. Lianas have myriad effects on plant and animal communities, as well as on emergent properties of forests, such as carbon and nutrient cycling (e.g. van der Heijden *et al*., **2013**, **2015**; Schnitzer *et al*., **2015b**,**c**). Therefore, by including lianas in the study of tropical forest ecology we gain insight into the ecology and functioning of the entire ecosystem.

Figure 1. Lianas climbing into the canopy (a, b) and lianas in the forest understory of a seasonal tropical forest in central Panama (c, d).

Box 1. What are lianas?

Lianas are woody vines that, similar to trees (and unlike epiphytes and hemi-epiphytes), remain rooted in the ground their entire lives (Schnitzer & Bongers, **2002**). Lianas are characterized primarily by their use of trees and other lianas to ascend to the forest canopy (Fig. 1). Lianas are particularly abundant and diverse in tropical forests, where they commonly compose 25% of the rooted woody stems and 35% of the woody plant species (Schnitzer *et al*., **2012**, **2015a**). In terms of biomass, however, lianas contribute very little compared with trees (< 5%), presumably because of their slender stems and low wood volume (e.g. Schnitzer *et al*., **2014**). Lianas and climbing plants are present in one-third of all angiosperm orders and in > 40% of angiosperm families worldwide (Gianoli, 2004, **2015**). They are often called one of the most apparent physiognomical differences between tropical and temperate forests because of their prevalence in tropical forests and relative paucity in temperate forests (Schnitzer & Bongers, **2002**).

Although there are exceptions, lianas prefer high-light conditions, such as those found at the top of the forest canopy, where they deploy the majority of their leaves above those of their host trees (Avalos & Mulkey, **1999**; Rodriguez-Ronderos *et al*., **2016**). Lianas also capitalize on the high-light environments after land abandonment, in treefall gaps, and at forest edges, where they are found in unusually high densities (Barry *et al*., **2015**;

Schnitzer, **2015b**; Campbell *et al*., **2018**). Compared with trees, lianas have thin stems and support a large amount of leaves per stem diameter, and thus lianas need a relatively large and efficient vascular system to supply water and nutrients to those leaves (Wyka *et al*., **2013**; Isnard & Feild, 2015). Lianas are therefore accurately depicted as relatively slender-stemmed plants that climb host trees to the top of the forest canopy where they deploy their relatively large mass of leaves.

The study of ecology, however, is more than the effect of the environment on an organism (*sensu* Grinnell, **1917**); it also includes the effects of organisms on their environment (*sensu*Elton, **1927**). By understanding how an organism affects its environment we gain insight into that organism's resource requirements, consumption rates, and the identity of interacting organisms (e.g. competitors, mutualists, parasites), information that is critical for testing a wide range of theory in population, community, and ecosystem ecology. Though this aspect of ecology has been tested extensively in grassland ecosystems (e.g. Tilman *et al*., **2014**), in forests it remains poorly tested experimentally for most plant groups except for lianas. To date, there have been at least 64 liana removal studies, which have quantified the effects of lianas on tree performance, forest diversity, and ecosystem-level carbon uptake and storage (Estrada-Villegas & Schnitzer, **2018**). Many of these studies also have addressed theory on plant population demography, the evolution and maintenance of animal diversity, and liana-mediated trophic interactions among producers, herbivores, and predators (e.g. Lambert & Halsey, **2015**; Schnitzer *et al*., **2015b**,**c**; Yanoviak, **2015**; Adams *et al*., **2017**; García León *et al*., **2018**; Visser *et al*., **2018a**).

In this review, I synthesize the exciting new findings in liana ecology. I emphasize select recent publications that pertain to the use of lianas to test ecological theory, rather than an exhaustive literature review, which can be found elsewhere (e.g. Schnitzer & Bongers, **2002**; Isnard & Silk, **2009**; Paul & Yavitt, **2011**; Wyka *et al*., **2013**; Schnitzer *et al*., **2015c**; Estrada-Villegas & Schnitzer, **2018**). I begin the review by first defining lianas (Box **1**) and then including a brief history of liana ecology (Box **2**), with the purpose of providing a historical context for the study of lianas, as well as confirming common perceptions and dispelling common misconceptions about liana ecology. In Section **II.**, I discuss how fundamental theories in ecology are being tested with lianas, particularly the maintenance of species diversity and the distribution of plants. Lianas appear to respond differently than trees to abiotic and biotic drivers of plant abundance and distribution (e.g. Ledo & Schnitzer, **2014**), and thus recent studies in liana ecology are providing new insights into the mechanisms that explain the abundance and distribution of plant species. Ultimately, I suggest that a single, scalable mechanism can explain both the distribution of lianas and the maintenance of their diversity (Section **III.**).

Box 2. A brief history of the study of liana ecology

Scientific interest in lianas can be traced back to early explorers and naturalists, such as Alexander von Humboldt, Charles Darwin, and Richard Spruce. In contemporary forest ecology, however, the study of trees has remained the central focus, while liana ecology has often ignored (Schnitzer & Bongers, **2002**; Isnard & Silk, **2009**; Wyka *et al*., **2013**; Schnitzer *et al*., **2015c**). For example, of the dozens of 50-ha forest plots established worldwide over the past 35 yr (Anderson-Teixeira *et al*., **2015**), all have focused on trees. Only the study on Barro Colorado Island in Panama included lianas ≥ 1 cm diameter across the entire 50 ha (Schnitzer *et al*., **2012**, **2015a**), with a few other large plots including lianas at more restricted spatial scales (Bongers & Ewango, **2015**; Burnham & Romero-Saltos, **2015**; Thomas *et al*., **2015**). The omission of lianas in these studies has also omitted their contribution to the study of fundamental ecological theory. Thus, the common perception that lianas are vastly understudied compared with trees has merit. Nonetheless, recent decades have seen a surge in studies on liana ecology (Schnitzer *et al*., **2015b**), including in-depth investigations of ecological theory (e.g. Schnitzer & Carson, **2001**; Dalling *et al*., **2012**; Ledo & Schnitzer, **2014**; Muller-Landau & Pacala, **2018**; Visser *et al*., **2018a**,**b**).

By contrast, the effects of lianas on their environment is exceptionally well studied. Over the past 90 yr, at least 64 published liana-cutting experiments have been published, making lianas one the most commonly manipulated elements in tropical forest ecology (Estrada-Villegas & Schnitzer, **2018**). Collectively, these studies demonstrate both the overwhelmingly negative effects of lianas on nearly all metrics of tree performance (recruitment, growth, survival, reproduction), and the direct and indirect positive effects on forest plant and animal communities (e.g. Schnitzer *et al*., **2015b**; Adams *et al*., **2017**). Thus, contemporary studies on lianas are advancing our understanding of ecological theory in terms of the effects of the environment on lianas, and especially the effects of lianas on their environment.

In Section **IV.**, I review the effects of lianas on their environment, which is a uniquely well-developed area of tropical forest research. I discuss the effects of lianas on key forest resources, as well as on tree growth and performance, and how lianas influence whole-forest carbon dynamics. In Section **V.**, I discuss how lianas have the potential to stabilize or destabilize tree species coexistence by having a stronger negative effect on some tree species than others. In Section **VI.**, I review the potentially important role of lianas in complex trophic interactions, which is a nascent area of study that may reveal positive contributions of lianas to tropical forests. In particular, lianas may maintain animal diversity by increasing the structural complexity of the environment (*sensu* Huffaker, **1958**), as well as potentially mediating competitive and trophic interactions (*sensu* Paine, **1966**). In the final section (Section **VII.**), I explore some of the next big challenges in liana ecology, emphasizing why these challenges are of interest to all ecologists. My ultimate goal is to persuade ecologists to move beyond thinking about lianas as a unique tropical curiosity and to recognize lianas as a diverse polyphyletic plant group that is advancing our understanding of fundamental ecological theory.

II. Testing ecological theory: effects of the environment on lianas

1. The maintenance of liana species diversity

Multiple theories have been investigated to explain the maintenance of liana species diversity; to date, however, strong support has been found only for disturbance (e.g. Putz, **1984a**; Schnitzer & Carson, **2000**, **2001**; Babweteera *et al*., **2001**; Dalling *et al*., **2012**; Ledo & Schnitzer, **2014**; Campbell *et al*., **2018**). For example, in a Malaysian tropical forest, Magrach *et al*. (**2016**) reported that liana species richness was higher in disturbed forests than in primary forests (see also DeWalt *et al*., **2000**). Two recent studies from Barro Colorado Island (BCI) in Panama compared the relative strength of multiple putative diversity-maintenance theories and found strong support only for natural disturbance as a mechanism to maintain liana diversity (Dalling *et al*., **2012**; Ledo & Schnitzer, **2014**). These studies utilized the spatially explicit liana dataset from the BCI 50-ha plot, which was collected in 2007 with a survey of *c*. 67 500 rooted liana stems (≥ 1 cm diameter) comprising 162 species (Schnitzer *et al*., **2008a**, **2012**, **2015a**). Dalling *et al*. (**2012**) examined the diversity and distribution of the 82 most common liana species in relation to topographic habitat variables and 13 soil chemistry variables. They found that treefall gaps, more than any other variable, explained the diversity of lianas, and that 63% of the liana species examined had a significant affinity for gaps. Whereas soil chemistry and distinct habitat type had a clear influence on tree diversity at this site (e.g. John *et al*., **2007**), these factors had a relatively small influence on liana diversity (Dalling *et al*., **2012**; see also Pasquini *et al*., **2015**).

Ledo & Schnitzer (**2014**) used the most common 52 liana species in the BCI 50-ha plot dataset to compare the relative strength of three putative theories to explain the maintenance of liana species diversity: (1) conspecific negative density dependence; (2) habitat specialization; and (3) disturbance. They found that liana diversity was significantly higher in treefall gaps than in the intact (closed canopy) understory, even when controlling for stem density, thus indicating that treefall gaps maintain liana diversity in this forest (see also Schnitzer & Carson, **2001**). Ledo & Schnitzer (**2014**) also reported that disturbance was the most powerful explanatory variable for the distribution of most liana species, whereas conspecific negative density dependence and habitat specialization (apart from treefall gaps) had only a minor influence (Box 3).

One of the classic hypotheses for how treefall gaps maintain species diversity is the idea of within-gap resource partitioning (e.g. Ricklefs, **1977**). Although liana species likely vary in their ability to take up resources in gaps, and resource partitioning theoretically could explain liana diversity in gaps, there is not yet compelling evidence that lianas actually partition resources (Schnitzer & Carson, **2001**). In fact, there is little direct empirical evidence that lianas compete with other lianas at all. However, considering their strong negative effect on trees (reviewed by Toledo-Aceves, **2015**; Estrada-Villegas & Schnitzer, **2018**), it would be surprising if lianas did not compete with each other for both light and belowground resources.

Ledo & Schnitzer (**2014**) suggested that treefall gaps provide a resource-rich regeneration niche (*sensu* Grubb, **1977**) for liana establishment and growth. They hypothesized that disturbance may elevate the density of most liana species, allowing them to persist and proliferate until the next disturbance, thus increasing the likelihood that species are retained in the community. Furthermore, by killing their host trees, lianas may serve as niche constructors (Laland *et al*., **2016**), creating the very environment that maintains their abundance and distribution.

Another hypothesis to explain how gaps maintain liana diversity is that the high availability of trellises in gaps, particularly on the gap edge, facilitates liana recruitment, growth, and survival, thus increasing liana diversity in gaps (e.g. Williams-Linera, **1990**; Chittibabu & Parthasarathy, **2001**; Campbell *et al*., **2015**). Putz (**1984a**) found that height growth increased substantially for four of the five liana species examined after they were supplied with trellises, suggesting that the availability of trellises contributes to liana recruitment in gaps. The exact mechanisms that maintain liana diversity following disturbance are still being investigated, but consistently higher liana diversity following disturbance indicates that liana diversity is maintained by disturbance, whereas other mechanisms, including those that maintain tree diversity, appear to have far less influence on liana diversity (Box 3).

Box 3. Diversity of lianas is maintained by different mechanisms than their host trees

Liana diversity appears to be maintained largely by disturbance, but not by either conspecific negative density dependence (CNDD) or soil attributes. For example, Ledo & Schnitzer (**2014**) reported that lianas on Barro Colorado Island (BCI), Panama, had a strong affinity with canopy disturbance. However, 81% of the 52 most common liana species on BCI had a clumped distribution pattern, which is inconsistent with CNDD. Furthermore, habitat specialization explained only a small percentage of liana species diversity (Ledo & Schnitzer, **2014**). Dalling *et al*. (**2012**) reported that only 21% of the most common 82 liana species on BCI were associated with soil chemistry. The ability to produce copious clonal stems may allow many liana species to capitalize effectively on disturbance while resisting disease-causing agents of CNDD and avoiding the need to become soil specialists (Schnitzer *et al*., **2012**; DeWalt *et al*., 2014; Ledo & Schnitzer, **2014**).

By contrast, disturbance may play a much smaller role in maintaining local tree species diversity, despite the enormous amount of literature on the role of treefall gaps in the maintenance of tropical tree diversity (Brokaw & Busing, **2000**; Schnitzer *et al*., 2008b). Instead, tree diversity appears to be maintained by multiple mechanisms. To date, studies have provided empirical evidence to support the maintenance of tree species diversity by both CNDD (e.g. Mangan *et al*., **2010**; Ledo & Schnitzer, **2014**; LaManna *et al*., **2017**) and edaphic characteristics and resource availability (John *et al*., **2007**; Condit *et al*., **2013**; Johnson *et al*., **2017**; Turner *et al*., **2018**). Therefore, liana species diversity appears to be maintained by disturbance, whereas their host trees are maintained largely by the combination of CNDD and habitat specialization.

2. The local, regional, and pantropical distribution of lianas

Within-forest (local) liana distribution (i.e., liana density), similar to liana diversity, is tightly correlated with such disturbance as treefall gaps, forest fragmentation, and young forest regenerating following agriculture or logging (e.g. Putz, **1984a**; DeWalt *et al*., **2000**; Schnitzer *et al*., **2000**; Dalling *et al*., **2012**). For example, Campbell *et al*. (**2018**) reported that liana density was particularly high on tropical forest edges compared with the forest interior (see also Laurance *et al*., **2001**; Londré & Schnitzer **2006**). In young forests that were previously used for agriculture and grazing, lianas can accumulate so rapidly that liana density in forests as young as 5 yr old can exceed the density of lianas in nearby old-growth forests (Barry *et al*., **2015**). In old-growth forests, liana density is far higher in treefall gaps than in adjacent intact (closed-canopy) forest (e.g. Schnitzer & Bongers, **2002**; Schnitzer *et al*., **2008a**,**b**; Dalling *et al*., **2012**). Thus, the link between liana distribution and disturbance at the local level is well supported empirically.

Among tropical forests (regionally and pantropically), liana density increases with decreasing mean annual precipitation and increasing length of the dry season (Schnitzer, **2005**; DeWalt *et al*., **2010**, **2015**). By contrast, trees (and most other organisms) tend to increase in abundance with increasing rainfall (Schnitzer, **2005**, figure 2). Therefore, liana density *relative to trees* increases much faster with decreasing mean annual precipitation than does absolute liana density. Gentry (**1991**) first documented the decrease in liana abundance with increasing rainfall for individuals ≥ 2.5 cm diameter in tropical forests around the world using ten $2 \times 50\ m^2$ plots per forest. Schnitzer (**2005**, **2015a**) further documented the pattern across the rainfall gradient along the isthmus of Panama and also pantropically using Gentry's data. DeWalt *et al*. (**2010**, **2015**) confirmed the negative relationship between liana density and mean annual precipitation using a series of large plots distributed across the tropics. Furthermore, DeWalt and colleagues found that liana abundance increased with dry season length, a parameter that may capture the seasonal stress that plants experience better than mean annual rainfall alone. In a recent study across the isthmus of Panama, Manzané-Pinzón *et al*. (**2018**) concluded that soil moisture availability, not mean annual rainfall or seasonality per se, was a stronger driver of liana distribution. Specifically, they found that limestone-soil forests (with low soil moisture-holding capacity) that received relatively high mean annual rainfall had much higher liana density than nearby laterite-soil forests with higher soil moisture. Furthermore, liana density and species composition in high-rainfall limestone-soil forests were more similar to geographically distinct dry forests than to nearby laterite-soil forests. Consequently, within forests, liana abundance tends to be high in disturbed areas, whereas among forests, liana abundance, particularly relative to trees, increases with the intensity of seasonal water stress.

III. A unified explanation for liana distribution and the maintenance of liana diversity

The distribution of lianas and the maintenance of liana diversity may both be explained by a single, scalable mechanism. Lianas grow particularly well during conditions of high light and severe and prolonged water stress, such as during the dry season in highly seasonal forests and following disturbance. Seasonal droughts can commonly last for 4–5 months, which gives lianas an extended period of high growth each year, which they lack in aseasonal, ever-wet forests. Furthermore, lianas grow far better than competing trees under these stressful conditions. Trees cannot fully take advantage of high dry-season light because they suffer more than lianas from the lack available soil moisture. Over decades, these additional months of high growth each year should result in higher liana abundance (both in absolute terms and relative to trees) in seasonal forests compared with wet, aseasonal forests. That is, both the absolute abundance of lianas and liana abundance relative to trees will be highest in seasonal forests, where lianas have a growth advantage and trees do not, compared with aseasonal, ever-wet forests, where lianas lack a seasonal growth advantage (SGA; Schnitzer, **2005**, **2015a**; Swaine & Grace, **2007**). Therefore, the ability of lianas to grow particularly well (and better than trees) during seasonal drought may explain their distribution regionally and pantropically, as well as with latitude and with altitude (Box **4**).

Box 4. Physiological constraints on the latitudinal and altitudinal distributions of lianas

Liana abundance and diversity peak in lowland tropical forests, and both decrease precipitously with increasing altitude and latitude (Schnitzer, **2005**, **2015a**). For example, liana species richness of North and South America was far lower in temperate latitudes than in the tropics (Schnitzler *et al*., **2016**). Liana abundance in both Chile and New Zealand decreased linearly with increasing altitude, from up to 35% of the species at low altitudes to complete absence in high-elevational forests (Jiménez-Castillo *et al*., **2007**).

The same functional characteristics of lianas that are advantageous in seasonal lowland tropical forests may also explain the precipitous decrease in liana density and diversity with increasing latitude and altitude. That is, the large vessels and acquisitive vascular system that give lianas an advantage in seasonal tropical forests become maladaptive in the freezing temperatures associated with higher latitudes and altitudes (Schnitzer, **2005**, **2015a**). If water inside the liana vascular system freezes, lianas can experience freeze–thaw embolism, which forms after the water changes from a solid to a liquid form, resulting in the loss of hydraulic conductivity (Sperry *et al*., **1987**). Jiménez-Castillo & Lusk (**2013**) examined hydraulic performance of lianas and trees in a high-elevation forest in Chile and found that the prevalence of winter freeze–thaw embolism was more than two times higher in lianas than in co-occurring trees. High altitudes in the tropics can present an additional problem: they are often rainy and shrouded in clouds and mist, which, like ever-wet tropical lowland forests, have low light and thus provide disadvantageous conditions for liana proliferation. Thus, the functional characteristics of lianas that are beneficial in seasonal lowland tropics become maladaptive at high altitudes and latitudes, thus explaining why lianas decrease with increasing latitude and altitude.

The SGA hypothesis was invoked initially to explain the unique distribution of lianas across forests regionally and pantropically (Schnitzer, **2005**). However, the SGA hypothesis can be extended to explain the maintenance of liana species diversity by disturbance, as well as local (within-forest) liana distribution. Specifically, at the local scale, treefall gaps, forest edges, and young (post-agricultural and post-grazing) forests provide an environment that is similar to that of seasonal forests: high solar radiation combined with high temperature, and low relative humidity (i.e., high vapor pressure deficit, VPD). Lianas rapidly colonize these disturbed areas via high seed rain (Puerta-Piñero *et al*., **2013**) and by rapidly producing multiple clonal stems in the high-light environment (Schnitzer *et al*., **2000**, **2012**, **2015a**). However, colonization may be only part of the explanation for liana proliferation following disturbance; lianas also appear to have higher rates of photosynthesis and growth than co-occurring trees in post-disturbance conditions (C. Smith-Martin *et al.,* unpublished). The ability of lianas to thrive in the high-light and high-VPD post-disturbance environment may explain the particularly high liana density and diversity in disturbed areas, as well as the local, within-forest distribution of lianas. Thus, this single mechanism may explain the maintenance of liana species diversity within forests and liana distribution at multiple scales.

1. Evidence for the SGA hypothesis to explain liana distribution and diversity maintenance

Evidence supporting the SGA hypothesis to explain the distribution of lianas has been accruing over the past decade. The initial indication that lianas were more active during seasonal drought than co-occurring trees were was based on phenological observations. Specifically, in some forests, a much larger proportion of liana species maintained their leaves during the dry season than tree species (Putz & Windsor, **1987**; Kalácska *et al*., **2005**). More recently, direct measurements of gas exchange (photosynthesis) and plant water status (water potential) during both dry and wet seasons revealed that lianas photosynthesize more and maintain better water status during seasonal drought than co-occurring trees. For example, in a seasonal tropical forest in Xishuangbanna, China, Cai *et al*. (**2009**) examined photosynthesis and gas exchange in 18 liana species and 16 tree species. They found that lianas were able to fix more carbon than trees did during seasonal drought and did so more efficiently in terms of water and nitrogen use. Also in Xishuangbanna, Zhu & Cao (**2009**) reported that liana species had higher maximum photosynthesis, higher hydraulic conductivity, and higher pre-dawn water potential than trees during seasonal drought, indicating that lianas were able to maximize photosynthesis while maintaining healthy water status during the dry season. In this same region of China, Chen *et al*. (**2015**) reported that liana species exhibited far higher water potential than trees during the dry season in a karst-soil forest that had very low water-holding-capacity soils. In an old-growth forest in French Guiana, Maréchaux *et al*. (**2017**) examined 247 trees and 57 lianas (individuals) and reported that lianas had a stronger seasonal osmotic adjustment than trees, concluding that lianas likely had an advantage in drier conditions.

In an experimental common garden study in Panama, C. Smith-Martin *et al*. (unpublished) found that lianas maintained higher photosynthesis and higher water potential than co-occurring trees did during both wet and dry seasons, with far greater differences during the dry season. The common garden study was located in an open, sunny, high-light, and high-VPD environment that was similar to an abandoned field or a large forest gap, thus supporting the idea that lianas grow better than trees do in stressful post-disturbance environments (see also Chen *et al*., **2015**). Furthermore, these authors also provided supplemental water to lianas and trees during consecutive dry seasons and found that tree growth increased considerably with dry-season irrigation, whereas liana growth did not, concluding that trees suffered far more seasonal water stress than lianas. Collectively, these studies indicate that lianas perform better than co-occurring trees in disturbed areas and during seasonal drought – fundamental requirements of the SGA hypothesis.

While proxies of growth, such as photosynthetic rate and water status, support the SGA hypothesis, a more direct and confirmational measurement of the SGA hypothesis is whether lianas actually grow more than trees during seasonal drought. In central Panama, Schnitzer (**2005**) measured the height growth of saplings of 10 liana species and 12 tree species in the understory of an old-growth forests during consecutive wet and dry seasons and found that lianas grew seven times taller than trees during the dry season, and only two times taller than trees during the wet season. In a recent and more definitive study in a nearby forest in central Panama, S. A. Schnitzer & G. M. F. van der Heijden (unpublished) followed the dry-season and wet-season diameter increment of 648 canopy lianas (> 5 cm diameter) and 1117 canopy trees (> 10 cm diameter) for 5 yr (2011–2016). They found that liana diameter growth rate was far higher during the 4-month dry season than during the wet season, confirming that lianas thrive during drought. In fact, the absolute diameter growth of lianas during the 4-month dry season was as much as the entire 8-month wet season. By contrast, tree diameter growth rate was far higher during the wet season, and absolute dry-season tree growth was only one-quarter of the wet-season growth. Furthermore, during the exceptionally dry el Niño dry season of 2016, trees essentially stopped growing, while liana growth was the same as the previous four, less severe dry seasons (S. A. Schnitzer & G. M. F. van der Heijden, unpublished). These data strongly support the SGA hypothesis to explain the local, regional, and global distribution of lianas, as well as the maintenance of liana species diversity.

2. The mechanisms behind vigorous liana growth in arid conditions

One hypothesis for how lianas grow and maintain healthy water status when water is limiting and VPD is high is that, compared to trees, lianas have well-developed root systems, which allow them to take up water better than co-occurring trees (Holbrook & Putz, **1996**; Tyree & Ewers, **1996**; Schnitzer, **2005**). For example, Chen *et al*. (**2015**) used water isotope ratios in lianas and trees and found that during the dry season, the proportion of deep soil water (151–250 cm depth) that was used by the plants was 43% higher for lianas than for trees, indicating that lianas had the capacity to take up water from deeper soil depths. In a Panamanian tropical forest, Andrade *et al*. (**2005**) used deuterium isotopes to measure the depth at which lianas accessed water during the dry season and reported that lianas were able to access deep soil moisture during the dry season, whereas not all tree species were able to do so (Meinzer *et al*. **1999**). Studies examining liana rooting depth and root hydraulic capacity reported that some liana species are extremely deeply rooted and can have a particularly large root diameter in relation to their stem diameter (Tyree & Ewers, **1996**; Restom & Nepstad, **2004**).

At some level, lianas must have access to water during the dry season, otherwise it would be impossible for them to photosynthesize and grow. However, not all studies found support for the deep root hypothesis. In French Guiana, De Deurwaerder *et al*. (**2018**) used stable water isotopes to evaluate the soil depth at which lianas and trees acquired water and found that lianas used shallow water sources during the dry season, whereas co-occurring trees used deeper water sources. C. Smith-Martin *et al*. (unpublished) harvested liana and tree roots and also did not find support for the deep root hypothesis, even though lianas had better water status during the dry season than trees did. Thus, it remains unclear whether lianas are tapping into deeper sources of water during seasonal drought than trees are. Liana rooting depth may ultimately depend on where soil moisture is most accessible during the dry season, and not solely on deep roots.

A second hypothesis for how lianas maintain vigorous growth during the hot and sunny conditions that are present during seasonal drought and following disturbance is that they can minimize the fundamental trade-off between photosynthesis and water loss (the safety–efficiency trade-off; Gleason *et al*. **2015**; DeGuzman *et al*., **2017**). One strategy to minimize the safety–efficiency trade-off is to have high intrinsic and integrated water use efficiency (WUE), which would maximize carbon assimilation and growth while minimizing water loss through transpiration. C. Smith-Martin *et al*. (unpublished) found that liana intrinsic WUE was 63% higher in lianas than in trees during the dry season, but only 2% higher in the wet season, demonstrating that lianas were assimilating far more carbon per water loss than were trees. Likewise, Cai *et al*. (**2009**) reported that lianas had higher integrated WUE than trees did during both the wet season and particularly during the dry season.

A second strategy to minimize the effects of the safety–efficiency trade-off is by operating at maximum photosynthesis earlier in the day than co-occurring trees. This 'fast and furious' strategy would allow lianas to attain a high rate of photosynthesis with less water loss. Early in the day, the ambient temperature is relatively low and the amount of water in the air is relatively high. As the tropical sun rises, however, temperature increases and humidity decreases, resulting in higher VPD. By quickly reaching maximum photosynthesis early in the day, when VPD is relatively low, and then closing their stomata to prevent excess water loss before VPD becomes high, lianas can maximize photosynthesis while preventing their xylem water tension from becoming dangerously negative. By closing their stomata early in the day, lianas would also have more time to recharge their vascular system before the following day.

There is some evidence to support the fast and furious hypothesis. For example, in a tropical forest on karst soil in Xishuanbanna China, Chen *et al*. (**2015**) reported that lianas reached and sustained maximum sap flux and photosynthesis much earlier in the morning than co-occurring trees did (see also Andrade *et al*., **2005**). **Chen *et al*.** also (2015) found that lianas were able to respond rapidly to increasing VPD during by quickly closing their stomata before they experienced excessive desiccation (see also Cai *et al*., **2009**). Lianas may be able to rapidly reach high photosynthetic rates because their highly conductive vascular system can transport a large volume of water to their distal branches and leaves (e.g. Meinzer *et al*., **1995**; Santiago *et al*., **2015**), rapidly replacing the water lost due transpiration and possibly delaying a dangerous increase of xylem tension.

Lianas also may use a number of other (nonmutually exclusive) strategies to avoid water stress. Lianas could utilize nonstructural carbohydrates (NSCs) to maintain healthy water balance within the stem and leaves. NSCs within stems and leaves may serve a critical function by allowing plants to efficiently move water within the stem, thus explaining why plants maintain NSCs even when carbon starvation is imminent (O'Brien *et al*., **2014**;

Hartmann & Trumbore, **2016**; Martínez-Vilalta *et al*., **2016**). Lianas may also have copious amounts of stored water in their trunks (capacitance), which they can use to minimize negative xylem tension; however, a recent study did not find support for the capacitance hypothesis (DeGuzman *et al*., **2017**). Alternatively, lianas could operate close to the boundaries of the safety–efficiency trade-off and, if embolisms occur, lianas could have the capacity to repair leaf-level embolism (Johnson *et al*., **2013**; DeGuzman *et al*., **2017**). Though these alternative mechanisms are all possible, they are not currently supported by compelling empirical data, and thus remain speculative. Whatever the mechanisms that allow lianas to outperform trees during seasonal drought, the evidence that lianas maintain better water status and grow better than co-occurring trees during seasonal drought and in hot, dry areas (e.g. following disturbance) is compelling, and it supports the SGA hypothesis to explain both liana distribution and the maintenance of liana diversity.

IV. Testing ecological theory: effects of lianas on the environment

Studying the ecology of lianas by examining their effects on the environment (Elton, **1927**) provides valuable information on liana resource consumption, the intensity of liana competition, the species with which lianas compete, and the effects of lianas on ecosystem processes and plant and animal community diversity. This information can be used to test a number of fundamental ecological theories, such as the keystone species concept (Paine, **1966**), top-down vs bottom-up control of ecosystem processes (Hairston *et al*., **1960**), biodiversity–ecosystem function (e.g. Tilman *et al*., **2014**), the role of ecosystem complexity in mediating species interactions (e.g. Huffaker, **1958**), and the relative roles of competition, parasitism, and facilitation in maintaining species diversity and determining species composition (e.g. Huston, **1979**; Tilman, **1982**; Bruno *et al*., **2003**; Lagrue *et al*., **2015**). Recent experimental studies provide a compelling assessment of the effects of lianas on forest resources (Box **5**), tree growth and physiological performance, whole-forest carbon uptake and storage, and tree reproduction and recruitment.

Box 5. Effects of lianas on forest resources

Cutting experiments have shown that lianas in tropical forests consume both light and soil moisture. For example, on Gigante Peninsula in Panama, Rodriguez-Ronderos *et al*. (**2016**) reported that 1 yr after cutting lianas the forest canopy intercepted *c*. 20% less light than control plots. In the same forest, Schnitzer & Carson (**2010**) found that lianas attenuated 18% of the light in treefall gaps. The amount of light that lianas consumed in three tropical dry forests in South America was lower than the estimates from Panamanian moist forests, but still substantial: between 4 and 12% (Gerwing, **2001**; Pérez-Salicrup, **2001**; César *et al*., **2016**).

Lianas also reduce soil moisture, competing intensely with trees during seasonal drought when soil moisture becomes limiting (reviewed by Powers, **2015**; Toledo-Aceves, **2015**). For example, on Gigante Peninsula, shallow soils (10 cm deep) dried more slowly over the first 4 months, and deeper soils (40 cm deep) increased by 25% in moisture 3 yr following liana cutting compared with control plots (Reid *et al*., **2015**). Tree sap flow also increased more after removing lianas in the dry season than the wet season, indicating that lianas were competing with trees for shallow to mid-depth soil moisture (Tobin *et al*., **2012**; Alvarez-Cansino *et al*., **2015**). In a glasshouse study, Toledo-Aceves & Swaine (**2008**) reported that belowground competition from lianas had a large negative effect on tree relative growth rate. In a liana-removal study in the understory of an African tropical forest, Schnitzer *et al*. (**2005**) reported that lianas had the largest negative effects on tree saplings via competition for belowground resources, probably for soil moisture, and that light competition played a relatively small role. Ultimately, lianas are adept at capturing both light and soil resources (moisture and nutrients), and the strength of their competitive effect on trees likely depends on which of these resources is most limiting.

1. Lianas and tree growth and physiological performance

Dozens of liana-cutting experiments over the past 90 yr provide compelling evidence of strong negative effects of lianas on tree performance (Estrada-Villegas & Schnitzer, **2018**). For example, in a seasonally inundated mature forest in the Darien region of Panama, Grauel & Putz (**2004**) found that the mean annual growth of *Prioria copaifera* canopy trees had doubled in the 5 yr following liana cutting compared with control plots. Similarly, in a semi-deciduous, subtropical forest in Argentina, liana cutting increased the growth rates of three of the four tree species studied (Campanello *et al*., **2007**).

In a series of liana-cutting experiments on the Gigante Peninsula, a 60-yr-old seasonal forest in central Panama, which is part of the Barro Colorado Nature Monument (hereafter Gigante Peninsula), lianas substantially reduced tree growth and physiological performance in both treefall gaps (Schnitzer & Carson, **2010**; Schnitzer *et al*., **2014**) and in nongap, closed-canopy forest (Tobin *et al*., **2012**; Alvarez-Cansino *et al*., **2015**; Wright *et al*., **2015**; Martínez-Izquierdo *et al*., **2016**). Cutting lianas in treefall gaps for 8 yr resulted in a 55% increase in tree growth rate and a 46% increase in tree recruitment compared with control gaps, where lianas were present (Schnitzer & Carson, **2010**). In closed-canopy forest, lianas substantially reduced tree sap flow velocity (a measure of short-term performance) and longer term growth rates, indicating that lianas place a heavy competitive burden on trees (Tobin *et al*., **2012**). Alvarez-Cansino *et al*. (**2015**) measured sap velocity for 92 canopy trees of seven species and found that sap velocity was 60% greater immediately after cutting lianas compared with control trees. This result was remarkable given that the treatment occurred near the end of the dry season when sap flow in the trees had been decreasing steadily due to the prolonged lack of rainfall (see also Tobin *et al*., **2012**). Tree diameter growth in that study was 25% greater 1 yr following liana cutting compared with control plots (Alvarez-Cansino *et al*., **2015**). Thus, lianas have a clear negative effect on tree growth and sap velocity. Furthermore, the strength of liana–tree competition may exceed that of tree–tree competition (Box **6**) because of the unique form of competition imposed by lianas (Box **7**).

Box 6. Explaining the strong negative effects of lianas on trees

Lianas have a uniquely strong negative effect on canopy trees for five main reasons. First, by growing into the canopy of their host trees, lianas deploy their leaves directly above those of their hosts, and proportionately displace their host's leaves (Kira & Ogawa, **1971**). This strategy differs from tree–-tree competition in the canopy, where crowns often do not overlap, and may explain why lianas have a particularly strong negative effect on host tree growth and survival (Estrada-Villegas & Schnitzer, **2018**). Second, once established in the canopy, lianas allocate more carbon to leaves than to stems compared with their host trees (Wyka *et al*., **2013**; van der Heijden *et al*., **2015**). Thus, even a relatively small liana can deploy a large area of leaves above the crown of its host tree. Moreover, a large liana can completely cover the crowns of multiple adjacent host trees (Putz, **1984a**; Fig. **1**b). Third, even relatively thin lianas can reach the forest canopy, where they displace tree leaves and, concomitantly, compete for soil resources. In a study along the isthmus of Panama, Kurzel *et al*. (**2006**) reported that lianas as small as 2.5 cm diameter had a 90% probability of being in the forest canopy. This means that even though lianas constitute only one-quarter of the woody stems, in many forests there may be far more canopy lianas than canopy trees, and these canopy lianas have an exceptionally strong negative competitive effect on their trees hosts. Fourth, the weight of lianas draping off of the top of a tree may impose considerable structural stress on trees (Schnitzer & Bongers, **2002**), forcing trees to invest more in stem thickness and density at the expense of height and leaf production. Fifth, lianas compete intensely with trees for belowground resources, particularly in areas where light is available (Schnitzer *et al*., **2005**; Toledo-Aceves, **2015**). Collectively, these unique characteristics of lianas result in a particularly intense form of competition with trees.

Box 7. Unique effects of lianas in tropical forests

Liana removal experiments have helped to quantify the strong negative effects of lianas on their tree hosts and on many different forest processes (Toledo-Aceves, **2015**; Estrada-Villegas & Schnitzer, **2018**). However, typical liana removal experiments have an obvious flaw: they cannot distinguish the unique negative effect of lianas on trees from the competitive release gained by the removal of any nearby vegetation. Several lines of evidence now indicate that lianas have a uniquely strong negative effect on trees and that lianas themselves cannot compensate for their negative effects on trees. For example, Tobin *et al*. (**2012**) conducted the first direct *in situ* comparison of the strength of liana and tree competition by comparing the effects of liana removal vs that of tree removal on canopy trees (controlling for the amount of biomass removed). They found that liana removal resulted in a strong increase in canopy tree sap velocity and growth. Removing the same biomass of nearby trees, however, had no detectable effect on tree sap velocity or growth.

The unique effect of lianas on canopy trees is also supported by the evidence that lianas have a much greater effect on canopy tree growth and biomass accumulation than would be predicted by their biomass. Schnitzer *et al*. (**2014**) reported that liana growth replaced only *c*. 25% of the biomass uptake that those lianas displaced in trees. That is, lianas significantly reduced tree biomass uptake, but those same lianas accumulated only one-quarter of the biomass that they displaced in trees (see also van der Heijden *et al*., **2015**). Lianas also significantly suppressed canopy tree reproduction; however, lianas themselves could not compensate for the amount of fruit production that they displaced in trees (García León *et al*., **2018**). Therefore, lianas have a uniquely strong negative effect on trees, and lianas often cannot compensate for the negative effects that they have on their host trees.

2. Lianas and forest biomass and carbon dynamics

The ability of lianas to reduce tree growth and survival results in a uniquely strong negative effect on forest-level biomass storage and uptake (Durán & Gianoli, 2013; van der Heijden *et al*., **2015**; Ledo *et al*., **2016**). In an experimental study on Gigante Peninsula, Schnitzer *et al*. (**2014**) removed all lianas in eight of 17 gaps for a period of 8 yr and found that tree biomass accumulation in liana-free gaps was 180% higher than in the control gaps (2.47 kg m^{-2} vs 0.88 kg m^{-2}, respectively). Also on Gigante Peninsula, van der Heijden *et al*. (**2015**) used a long-term liana removal experiment in large plots in closed-canopy forest and found that lianas decreased annual forest biomass accumulation by *c*. 75%, while concomitantly increasing carbon turnover. Specifically, in plots where lianas were present, leaves contributed 32% more and stems 34% less to aboveground net primary productivity than in plots where lianas had been removed (leaves: 53% vs 40%, respectively; stems: 29% vs 44%, respectively). Because leaves turn over (and thus release their carbon) much faster than stems, lianas substantially increase forest-level carbon cycling. In a forest fragment in Brazil, César *et al*. (**2016**) found that tree sapling biomass increased by 50% 1 yr after cutting lianas. In a small-scale liana cutting trial in areas of particularly high liana infestation in the intact understory of a Tanzanian forest, lianas reduced the biomass increase in sapling trees (1–5 cm diameter) by more than 10-fold (Marshall *et al*., **2017**). Though the magnitude of the effects of lianas will vary with forest age, forest type, and liana abundance, the empirical data demonstrate that lianas substantially decrease annual carbon uptake and storage, as well as increase rates of carbon cycling in tropical forests.

3. Lianas and tree reproduction, seedling recruitment, and seedling survival

Reproduction and recruitment are critical processes in population demography (Harper, **1977**). Recent studies have shown that lianas substantially reduce tree reproduction and recruitment. For example, Kainer *et al*. (**2014**) reported that the reproduction of 78 Brazil nut trees (*Bertholletia excela*) in a forest reserve in Acre, Brazil, was 77% higher 10 yr after removing lianas than withcontrol trees (with lianas). On Gigante Peninsula, Panama, García León *et al*. (**2018**) examined the effect of lianas on tree community-level reproduction using 576 trees of

65 species and found that liana removal at the plot level resulted in 150% more canopy trees with fruits and 109% more canopy species with fruits. In addition, fruiting trees had 31% more of their canopy covered by fruits in the removal plots compared with trees in the control plots.

Lianas not only reduce tree reproduction, they also reduce seedling recruitment survival and diversity. In the Darien region of Panama, the mean seedling density of *P. copaifera* was nearly four times higher in plots where lianas had been cut than in control plots (Grauel & Putz, **2004**). Comparing tree recruitment in treefall gaps where lianas had been removed with control gaps where lianas were present on Gigante Peninsula, Schnitzer & Carson (**2010**) found that tree recruitment density and diversity were, respectively, 46% and 65% higher where lianas had been removed. They concluded that lianas may reduce niche competition among trees in gaps by limiting the number of species that regenerate. Martínez-Izquierdo *et al*. (**2016**) planted > 3000 replicate seedlings of 14 species into the eight liana-removal and eight control plots on Gigante Peninsula. They found that, 2 yr following liana removal, tree seedling survival was 75% greater, seedlings grew 300% taller, and seedling biomass was two times higher than in the control plots. Consequently, lianas reduce tree recruitment, growth, reproduction, survival, and diversity.

V. Theoretical effects of lianas on forest diversity

Lianas may have important effects on tree species diversity and coexistence (Magrach *et al*., **2016**; Visser *et al*., **2018b**). Specifically, lianas could stabilize or destabilize tree species coexistence depending on the relative strength of the negative effects of lianas on different tree species. Lianas could stabilize tree species coexistence by having a strong negative effect on competitively dominant tree species (*sensu* Tilman, **1982**), which prevents the dominant species from displacing competitively subordinate tree species. For example, by killing competitively dominant shade-tolerant trees, lianas may reduce the amount of competitive pressure on subordinate (less shade-tolerant) pioneer trees. Lianas may also increase gap formation, which creates regeneration sites for less-competitive pioneer tree species. Thus, lianas may serve as a keystone group (*sensu* Paine, **1966**, **1969**) because lianas would maintain community diversity by suppressing the competitive dominant, while directly contributing only a small fraction (< 5%) of the total plant biomass in tropical forests (Putz, **1983**; DeWalt & Chave, **2004**; Wyka *et al*., **2013**). The presence of lianas could therefore be a stabilizing factor for tree community diversity and composition, ultimately contributing to the maintenance of tree species diversity.

By contrast, lianas could decrease tree diversity if lianas have a stronger negative effect on competitively subordinate tree species, further disadvantaging these species relative to competitively dominant species. Under this scenario, the combination of pressure from lianas and from competitively dominant tree species would reduce the density of subordinate tree species, decreasing species evenness and species richness, ultimately decreasing tree diversity. Additionally, if lianas have a similarly strong negative effect on all tree species then lianas may decrease species richness by depressing tree density, which would lead to a greater chance of eliminating rare species from the local species pool.

A third possibility is that lianas could help maintain diversity by suppressing competition among all tree species (*sensu* Huston, **1979**). By reducing the ability of trees to uptake resources and thus reducing tree growth rates, lianas may reduce the speed at which trees displace each other, thus allowing tree species to coexist for much longer periods (Huston, **1979**). Because there is now overwhelming evidence that lianas have a substantial negative effect on tree performance (Toledo-Aceves, **2015**; Estrada-Villegas & Schnitzer, **2018**), these contrasting theoretical alternatives for how lianas can influence tree community composition and diversity emphasize the importance of determining whether the negative effects of lianas vary with tree species identity.

1. Do the effects of lianas on trees vary with tree species diversity?

Whether lianas have a stronger negative effect on some tree species than others remains controversial. Some studies have found that lianas have a similar negative effect on tree growth and survival regardless of the tree species examined. For example, on Gigante Pensinsula, Martínez-Izquierdo *et al*. (**2016**) reported that cutting lianas increased the mean growth and survival of 3136 seedlings comprising 14 tree species, but that species did not differ significantly in their responses to liana removal. In this same experiment, Alvarez-Cansino *et al*. (**2015**) examined the response of 92 canopy trees of seven species to liana removal and found that all species responded similarly and positively to liana removal.

By contrast, other studies have reported that the negative effect of lianas varied with tree species identity (Pérez-Salicrup & Barker, **2000**; Barker & Pérez-Salicrup, **2001**; Campanello *et al*., **2007**; Wright *et al*., **2015**). For example, studies have suggested that lianas have a stronger negative effect on shade-tolerant tree growth and survival than on shade-intolerant trees (Putz, **1984a**; Clark & Clark, **1990**; Schnitzer *et al*., **2000**; van der Heijden *et al*. **2008**), thus explaining why shade-intolerant tree species are often found growing without lianas. Shade-intolerant trees, these authors argued, could escape liana infestation by outgrowing lianas, minimizing the amount of lateral branching to prevent liana anchoring, and by producing large leaves that, when shed, could dislodge climbing lianas (Putz, **1984b**; Clark & Clark, **1990**).

Recent studies by Visser *et al*. (**2018a**,**b**) came to a different conclusion. Visser *et al*. used several long-term datasets from BCI on dozens of tree species and reported that the negative effect of lianas on tree species' population growth rates actually decreased with increasing tree shade tolerance. They argued that whereas shade-intolerant trees may indeed shed lianas, the shade-intolerant trees when infested suffer high mortality, and thus only shade-intolerant species without lianas survive. The presence of uninfested trees, therefore, may have led to the previously incorrect conclusion that shade-intolerant trees were resistant to liana infestation. The studies by Visser *et al*. (**2018a**,**b**) are insightful because they examined trees over a much longer period than did previous studies and they followed tree species population demography rather than tree growth rates. Nonetheless, whether lianas actually stabilize or destabilize tree species diversity and community structure remains an open question that is critical for understanding the effects of lianas on forest species diversity.

VI. Lianas and trophic interactions in forests

Lianas can provide critical resources to insects, birds, and mammals, thus enriching the animal community. High liana diversity may support a host of specialist insect species (e.g. Janzen, **1970**; Ødegaard, **2000**). For example, in a highly seasonal forest in central Panama, Ødegaard (**2000**) reported that an average of 47 beetle species were specialized on each liana species, and that beetle specialization was significantly higher for lianas than for trees in this forest. In a comprehensive review of 43 studies on liana–primate interactions, Arroyo-Rodriguez *et al*. (**2015**) reported that lianas can constitute more than 20% of the primate diet, and that primates utilized lianas mostly for fruits and leaves, but that they also ate liana flowers, nectar, stem, bark, and buds. Additionally, many liana species produce leaves, flowers, and fruits during the dry season, when their host trees do not, thus providing important seasonal resources for many animal species (Dunn *et al*., **2013**; Yanoviak & Schnitzer, **2013**; Arroyo-Rodriguez *et al*., **2015**).

Theoretically, more structural complexity in an ecosystem can increase diversity by stabilizing species interactions, such as predator–prey cycles (e.g. Huffaker, **1958**). The twisting and curling liana stems (Fig. **1**) may increase the structural complexity of tropical forests, providing perches, nesting opportunities, and enemy-free sites for many animal species (Kilgore *et al*., **2010**; Lambert & Halsey, **2015**; Michel *et al*., **2015**; Yanoviak, **2015**), as well as linking together the canopy of multiple trees (Putz, **1984a**,**b**; Garrido-Pérez *et al*., **2008**). To nonvolant animals, particularly invertebrates, an isolated tree that is not connected to other trees by lianas can be analogous to an island, because it is difficult to move to nearby trees over the ground (Ng, **1977**;

Yanoviak, **2015**). Isolated trees tend to have lower invertebrate diversity, presumably because there are fewer resources and a single aggressive species can easily displace other species (Yanoviak, **2015**; Adams *et al*., **2017**). However, lianas growing into multiple tree crowns can add a more diverse set of resources to those tree crowns, as well as effectively link the forest canopy together, which provides aerial pathways that are utilized by many animal species (Arroyo-Rodriguez *et al*., **2015**; Yanoviak, **2015**). For example, Adams *et al*. (**2017**) examined trees with and without connectivity from lianas and found that trees with lianas had 27% more ant species richness than liana-free trees did.

Lianas also may contribute to complex trophic interactions in tropical forests. The interaction between animals and trees may be mediated, to some degree, through the effects of lianas. For example, Neotropical forest trees commonly produce animal-dispersed seeds, whereas Neotropical lianas more commonly produce wind-dispersed seeds. By suppressing the production of larger and more nutritious animal-dispersed tree fruits and replacing them with relatively small and nutrient-poor wind-dispersed seeds (García León *et al*., **2018**), lianas may reduce food availability to many frugivores, possibly altering the relative importance of bottom-up and top-down control (*sensu* Hairston *et al*., **1960**), and thus influencing trophic interactions. Consequently, lianas may have an enormous effect on animal communities and on trophic interactions, and recent studies are now beginning to elucidate these effects.

VII. Unresolved challenges in liana ecology

The study of liana ecology has advanced our understanding of ecological theory. We now have compelling evidence that disturbance strongly influences the maintenance of liana species diversity, and that mechanisms that are important for tree diversity appear to have only a relatively small influence on lianas themselves. Treefall gaps and other forms of disturbance may provide a regeneration niche for lianas due to the ability of lianas to proliferate in hot, dry environments (Ledo & Schnitzer, **2014**). However, whether liana species compete to the level where they partition resources in gaps (or in the intact forest) is unknown and is a critical missing component in determining the effects of the environment on the maintenance of liana species diversity. Furthermore, whether disturbance maintains lianas in all forest types also remains an open question. The majority of the tests of the maintenance of liana species diversity have been conducted in seasonal tropical forests. However, the liana species that excel in highly seasonal forests may be pre-adapted to respond to disturbance, and the degree to which lianas in wet and dry forests respond to disturbance is not well understood.

There is now ample empirical support for the SGA hypothesis to explain the distribution of lianas. However, various details about the mechanisms responsible for liana distribution remain poorly understood. Recent studies have shown that lianas maintain healthy water status during seasonal drought, but how lianas find sufficient amounts of water to accomplish this feat remains unclear. Do lianas tap into deep sources of water, as has been hypothesized previously (Schnitzer, **2005**; Chen *et al*., **2015**), or do they explore a larger volume of the shallow soil surface (e.g. De Deurwaerder *et al*., **2018**)? Are lianas employing a strategy of early-morning photosynthesis combined with strong stomatal control that allows them to avoid excessive dehydration (e.g. the fast and furious hypothesis)? Do lianas frequently embolize and then clear these embolisms using a combination of positive root pressure and NSCs (Johnson *et al*., **2013**)? These hypotheses are intriguing, but they have yet to be rigorously tested in multiple environments.

In terms of the effects of lianas on the environment, there is no doubt that lianas have an overwhelmingly negative effect on nearly every metric of tree performance. However, we know little about how different liana species vary in their functional traits and their ability to compete with trees (Ichihashi & Tateno, **2011**). Whether some liana species have a stronger competitive effect on trees than others is an important issue, because we currently have no estimate of ‘virulence’ of individual liana species, and thus the effects of lianas have to be modeled as if all liana species have a similarly negative effect on trees (Muller-Landau & Pacala, **2018**; Visser *et al*., **2018b**), which is likely to be an unrealistic assumption. Furthermore, studies on the effects of lianas on their environment have only recently begun to establish a rigorous link to fundamental ecological theory.

Quantifying how the effects of lianas vary with tree identity and functional characteristics remains an important open area of investigation. The theoretical predictions for the effects of lianas on tree community diversity and functioning may depend on whether the strength of the effects of lianas varies with tree species identity. Negative effects of lianas may vary predictably with tree species shade tolerance (Putz, **1984b**; Visser *et al*., **2018a**); however, the negative effects of lianas may also vary with other tree traits and life-history strategies, a topic that has not yet been thoroughly investigated. Furthermore, whether the effects of lianas actually stabilize or destabilize tree species diversity and community structure remains an important and yet unresolved question.

While many studies commonly refer to lianas as intense competitors with trees, we have very little information on whether trees actually compete with lianas. If not, the liana–tree interaction may be more appropriately considered to be parasitism rather than competition (Stewart & Schnitzer, **2017**). Whether lianas are better described as competitors or parasites of trees will ultimately depend on the reciprocal net negative population-level effects of lianas and trees on each other (Stewart & Schnitzer, **2017**). Because the theoretically predicted outcomes of competition and parasitism can be fundamentally different, and because lianas have a large negative effect on trees, understanding whether lianas are truly competitors or parasites of trees remains an important open question.

Lianas clearly influence certain animal groups (e.g. Michel *et al*., **2015**; Adams *et al*., **2017**); however, the net effects of lianas on most animal communities is still largely unknown. Additional research is necessary to determine whether lianas have net positive or negative effects on animal communities, how the effects of lianas vary among animal species, and how these effects vary with forest type and geographic location. Do lianas provide a fundamental service to the forest by providing a seasonal resource base to animals, which then serve to pollinate trees and other plant groups? Do the twisting and curving tangles of lianas in the forest understory and in the forest canopy provide a critical habitat for many forest-dwelling animals, or do lianas suppress animal populations by reducing canopy tree fruit production? The role of lianas in trophic interactions is a potentially exciting yet largely unexplored frontier, which could reveal a host of new ideas for how forest connectivity and complexity can maintain diversity and influence ecosystem functioning.

VIII. Conclusions

Over the past three decades, the study of lianas has moved from a largely natural history focus to one of testing fundamental ecological theory. These studies have demonstrated that both liana distribution and diversity may be maintained by a single, scalable mechanism. Tropical lianas are able to grow better than co-occurring trees when light is abundant and water stress prolonged – conditions associated with both seasonal drought and disturbance. The ability to grow better than competing species under stressful conditions gives lianas an advantage that, over time, results in an increase in their relative abundance compared with co-occurring trees. Fundamental differences in anatomy, physiology, and life-history strategies between lianas and trees have led to very different mechanisms that maintain their diversity and control their distribution across spatial scales.

Many studies have documented the effects of lianas on their environment, which has led to the understanding that lianas have both negative and positive effects on co-occurring plant and animal communities. Whereas the majority of liana manipulations have emphasized the strong negative effect on trees, a more nuanced interpretation includes the possibility that lianas may stabilize or destabilize interactions among competing trees, thus contributing to the maintenance of tree species diversity. Lianas also add a considerable amount of resources and structural complexity to forests, which enhances animal diversity. Lianas may influence trophic interactions by altering the resource base for many animal species, and lianas may provide critical resources for forest animals, which ultimately may influence multiple trophic interactions (e.g. pollination, competition, and predation). Consequently, lianas are an integral component of tropical forests, and understanding their ecology is critical for understanding the ecology of tropical forests. More important, the study of lianas is no longer restricted to tropical forest ecology; such study is now providing novel insights into fundamental ecological theory.

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