

What Determines the Abundance of Lianas and Vines?

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Climbing plants—a group that includes both lianas (woody) and vines (nonwoody)—are found in a majority of the world’s forests, at widely varying abundances. Climbing plants are more abundant in tropical than in temperate forests, in dry tropical forests than in wet tropical forests, and in younger forests and forest edges (Schnitzer 2005, DeWalt et al. 2015). The abundance of climbers is critically important to determining forest carbon stores and cycling (van der Heijden et al. 2015, Schnitzer 2018). Where there are more lianas and vines, trees grow more slowly, forests store less carbon, and forest structure is altered, with implications for the diversity and abundance of other plants and animals within the forest (Schnitzer et al. 2015). Further, the effects of lianas differ among tree species, and thus the relative performance of tree species depends on liana abundance (Muller-Landau and Visser 2019). Thus, the question of what determines the abundance of lianas and vines within a forest is central in forest ecology. Yet surprisingly, we have not yet answered the question of what determines the abundance of climbing plants in any forest, much less what explains variation in their abundance across forests and among tree species within forests.

Climbing plants have inherently lower investment in structural support than self-supporting woody plants (trees and shrubs). Trees invest a substantial part of their carbon and other resources in constructing and maintaining trunks and branches to compete for light. Lianas and vines, as structural parasites on trees, invest far less (Darwin 1865). This then poses a conundrum: Given that climbing plants receive similar benefits (light) at lower cost (stems), why aren’t they more common relative to trees? After all, common though they are, lianas and vines are much less abundant than trees in the vast majority of forests and are completely absent from other forests. There are parallels here to the classic question “why is the world green?” (Hairston et al. 1960). In both cases, we need to step back and recognize that the world as we are used to seeing it is not the only way it could be, and that the current state requires explanation.

A first answer to the question of why lianas and vines aren't more common might be that, as parasites, they depend on trees to be their hosts, and cannot themselves dominate forests. However, local patches in which lianas or vines dominate and the canopy is very low (e.g., liana-choked gaps) are found in many temperate and tropical forests, although they generally occupy only a small fraction of the landscape (Terramora et al. 1991, Foster et al. 2008). Further, there are so-called "liana forests" in French Guiana, Bolivia, Brazil, and elsewhere in the tropics, in which lianas dominate over large areas (e.g., Pérez-Salicrup et al. 2001, Foster et al. 2008, Tymen et al. 2016).

In this essay, we consider what mechanisms regulate and limit the abundance of climbing plants at different scales, and how these might contribute to explaining variation in their prevalence within and among forests. We say a mechanism *regulates* climber abundance if it introduces negative density-dependence that prevents climbers from increasing in abundance without bounds (Turchin 1995). By *limiting* factors, we mean both density-dependent and density-independent factors that affect the abundances at which climbers are regulated. For simplicity, we refer in the remainder of the text simply to lianas; however, almost all our arguments apply equally to vines.

We propose that liana abundance is regulated and limited at three distinct and interacting scales: in the proportion of trees infested with lianas; in the liana load within the crowns of individual host trees; and in the proportion of the landscape that is in a liana-dominated, low-canopy state. We suggest that a disease ecology or host–parasite ecology framework offers useful insights for understanding the first two scales. Thus, the proportion infested can be understood as a function of the rates at which uninfested trees are colonized and infested, the rates at which infested host trees lose lianas, and the demographic rates of infested and uninfested hosts. We suggest that the biomass of lianas within a tree crown (parasite load) can be understood in terms of selection for the highest reproductive number, expressed as new hosts infested per infested host (Anderson and May 1982), which necessarily must balance the benefits of higher liana load and associated resource pre-emption against the cost to the parasite of negative impacts this load imposes on its host (Ichihashi and Tateno 2011). Finally, the proportion of the landscape that is in a liana-dominated, low-canopy state doesn't fit within a disease ecology or host–parasite framework; it is as though a parasite had a free-living alternative lifestyle that competed directly with its host. In the remainder of this essay, we discuss what regulates and limits liana abundance at each of these scales in turn.

Proportion of Trees Infested with Lianas

We can explain the proportion of trees infested with lianas in fundamentally the same way that we explain the prevalence of a disease or parasite in a host population. The proportion of infested trees must depend on (1) the *liana colonization rate*, the rate at which liana-free trees become infested (analogous to disease transmission); (2) the *liana loss rate*, the rate at which infested trees lose lianas (analogous to recovery from an infectious disease); and (3) the *host demographic rates*, specifically mortality and recruitment of infested and uninfested hosts (Fig. 1A). If these rates and their dependence upon the density and frequency of infested and liana-free trees are known, then we can solve the corresponding differential equations for the expected stable equilibrium proportion of trees infested with lianas, and the solution will illuminate exactly how the proportion infested relates to the parameters determining liana colonization, liana loss, and host demographic rates.

It is useful to frame this discussion with reference to a simplified model. This enables us to discuss factors in terms of their influences on parameters of the simplified model, or deviations from the simplified model forms. Let I be the number of liana-infested trees, and S the number of liana-free trees susceptible to liana colonization. In the simplest formulation, all liana-free trees are susceptible, and thus $S = N - I$, where N is the total number of trees, assumed constant for simplicity. A simple frequency-dependent model for the liana colonization rate (liana-free trees infested per unit of time) is $\beta SI/N = \beta I(N - I)/N$, where β is a constant that reflects the liana colonization pressure per infested tree (Fig. 1B). The simplest model of the liana loss rate (liana-infested trees losing lianas per time) is that it equals νI , where ν is a constant for the rate at which liana-infested trees lose lianas. And the simplest model for mortality of infested hosts is αI , where α is a constant infested tree mortality rate (Fig. 1C). This leads to the following differential equation for the number of infested individuals:

$$\frac{dI}{dt} = \beta I \left(\frac{N - I}{N} \right) - \nu I - \alpha I$$

Here, the proportion of trees infested by lianas is *regulated* by the negative density-dependence of colonization (the $N - I$ term): The number of trees newly colonized by lianas eventually declines as the availability of susceptible trees goes down. Under this model, the proportion of trees infested with lianas tends to a stable equilibrium,

$$\frac{\bar{I}}{N} = 1 - \frac{\nu + \alpha}{\beta}.$$

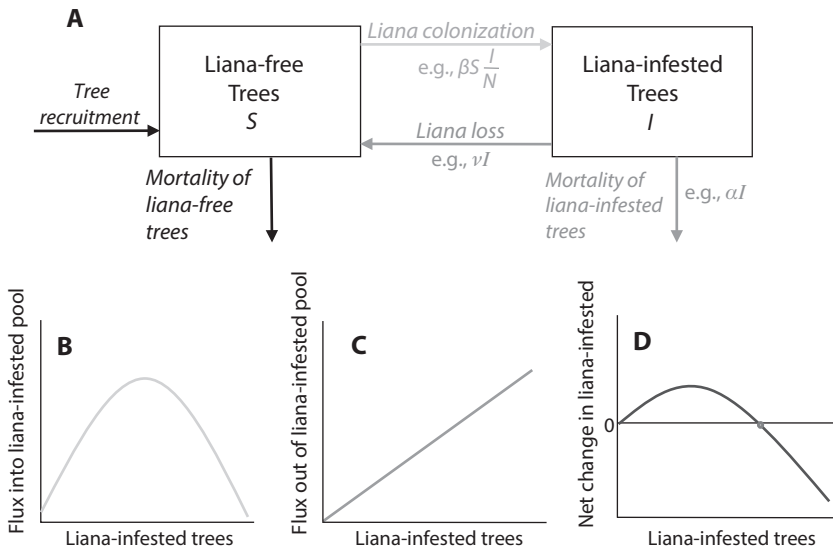


FIGURE 1. (Caption on facing page.)

The proportion infested increases with the liana colonization rate β , and declines with the liana loss rate ν and the infested tree mortality rate α ; thus, all three parameters can be said to *limit* the proportion infested.

We now discuss each of the three sets of underlying rates—liana colonization, liana loss, and host demography—and its controls. We thereby link the simplified model above to natural history knowledge about these processes.

Liana Colonization

In general, we expect the number of new trees infested in a forest stand to be a unimodal function of the total proportion infested, with an initial increase due to increased availability of lianas to do the colonizing, and an eventual decrease as the supply of liana-free susceptible trees dwindles (Fig. 1B). The height of the curve depends on liana reproductive success per infested tree, expressed in the simplified model through the parameter β . The point at which this curve returns to zero reflects the abundance of liana-free trees *susceptible* to colonization, which may be less than the total abundance of liana-free trees in the real world, unlike the simplified model. Any potential density- or frequency-dependence in reproductive success would result in deviations from the simplified model that alter the shape of the curve from a simple parabola. We treat each of these features of the curve in detail in the following paragraphs.

FIGURE 1. (A) A simple box model for the prevalence of liana infestation in a tree community. Under the assumption that the total number of trees remains constant, the proportion of trees infested with lianas depends only on the rate at which liana-free trees are colonized by lianas (light-gray arrow), and the rates at which liana-infested trees die or lose lianas (dark-gray arrows). More generally (if total tree number is not fixed), it will also depend on the mortality and recruitment rates of liana-free trees (black arrows). These rates can all take various functional forms; the simple examples discussed in the text are shown here. (B) The flux of trees into the liana-infested pool (newly infested trees per time) is expected to be a unimodal function of the number of trees infested with lianas. It depends on both the availability of liana-infested individuals to serve as a source of colonization (increasing part of the curve), and the availability of liana-free individuals susceptible to colonization (decreasing part of the curve). (C) The flux of trees leaving the liana-infested pool encompasses cases in which lianas are lost from the tree (tree transitions from liana-infested to liana-free) and death of liana-infested trees. Both of these fluxes are expected to be continuously increasing functions of the number of liana-infested trees; in the simplest case treated here they are proportional. (D) The combination of unimodal fluxes in and proportional fluxes out of the liana-infested tree pool leads the net change in liana-infested trees to be a hump-shaped function of the number of liana-infested trees, and thus to an expected stable equilibrium abundance of trees infested with lianas (point), below which the net change is positive, and above which it is negative. For the specific functional forms given in (A) and constant total population size N , the equilibrium proportion infested is $\bar{T}/N = 1 - (v + \alpha)/\beta$. All these curves and associated parameters will depend upon liana life history strategies (e.g., aggressive versus conservative, climbing mode), tree life history strategy (e.g., fast versus slow), and the environment. The peak of the colonization curve (B) may be increased by factors that increase liana fecundity, increase juvenile liana survival, increase trellises for lianas to climb to the canopy, and/or reduce tree defenses against lianas, depending on which factors limit liana infestation. The right-hand x-intercept of the colonization curve will be reduced by factors that reduce the proportion of liana-free trees susceptible to colonization. The steepness of the loss functions (C) and thus the magnitude of the outgoing flux will be decreased by factors that decrease the mortality of infested trees and decrease the rate of liana loss from infested trees, including less effective tree defenses to promote liana loss. Factors that increase the colonization flux or decrease the flux out of the infested pool will increase the equilibrium abundance of liana-infested trees.

The height of the colonization curve depends on what would be called *transmission* in disease ecology. Here, this reflects the combined influences of liana seed production and vegetative shoot production per host tree infested, and the odds that these offspring survive and succeed in finding and climbing a host tree. Seed production and vegetative shoot production per infested host depend closely on the liana load in the host tree—whether there are many liana leaves in favorable (sunlit) positions on the tree, or few in unfavorable (shaded) positions, for example. (The factors controlling liana load will be considered in the section Liana Load Within Individual Trees.) The colonization success per liana seed depends on liana regeneration requirements and the conditions in the forest understory—especially light levels—as well as on the availability of suitable trellises to the canopy along which the juvenile liana can grow. Different liana climbing strategies are limited to different substrates; for example, tendril climbers require small stems to grip, twining lianas cannot climb stems above a certain diameter; and adhesive climbers require a relatively rough surface and cannot move between branches or trees (Putz 1984b). The success per vegetative shoot running along the ground similarly depends on the availability of trellises, whereas the success of shoots deployed from one crown to another depends on sufficient proximity of other uninfested crowns (Putz 1984b), and thus can only fully be addressed with a spatially explicit model.

The point at which the colonization curve returns to zero depends on the proportion of liana-free trees that are susceptible to liana colonization. If all liana-free trees are susceptible to liana colonization, then the colonization rate reaches zero only when all trees are infested with lianas. However, some trees may be resistant to liana colonization. Canopy trees may be able to escape in size: If they grow a fat enough trunk and high enough lower branches sufficiently separated from other trees, then they cease to be amenable to colonization, at least by most types of lianas (Putz 1984a, Campbell and Newbery 1993). Trees may also be uncolonizable by virtue of possessing highly effective defenses against lianas, such as mutualist ants that clip liana tendrils (Janzen 1969, Tanaka and Itioka 2011). This uncolonizable host population parallels the resistant/recovered population in many disease models. In this case, the colonization curve will return to zero at a proportion infested equaling one minus the proportion of uncolonizable hosts.

There are several mechanisms that could introduce negative density-dependence to liana “transmission” beyond that due simply to the exhaustion of susceptible hosts, and thereby change the shape of the colonization curve. Much of liana transmission to new hosts is through vegetative propagation, which is short-distance (Schnitzer et al. 2012a). This local transmission results in clustering, such that trees close to liana-infested trees are more likely to be already infested, and less likely to be liana-

free and susceptible to colonization, than is the average for the larger forest stand (Schnitzer et al. 2012b). Insofar as liana infestation reduces tree reproductive success (Visser et al. 2017), higher densities of lianas may also lead to higher local abundances of tree species uncolonizable by lianas. Both of these mechanisms reduce liana reproductive success in areas of high liana densities.

On the other hand, there are other mechanisms by which liana reproductive success may increase with the proportion of trees infested, leading to positive density-dependence. The presence of liana-infested trees may change the environment in ways that increase colonization success and thereby introduce positive density-dependence. Liana-infested trees may be more likely to lose branches or experience die-back, increasing understory light and consequently tree and liana sapling survival, thereby increasing trellis availability and the probability that a liana seed or vegetative shoot will make it to the canopy. Some of the same factors that increase the proportion of trees infested also tend to increase mean liana loads per infested host (treated in the section *Liana Load Within Individual Trees*), and this in turn may increase liana reproductive success per infested host. Further, we hypothesize that higher liana abundance is likely to be associated with a greater incidence of host coinfection (more than one liana on a single host), and that this in turn may favor more aggressive liana strategies due to a tragedy of the commons (addressed in the section *Liana Load Within Individual Trees*). Such more aggressive strategies involve higher pre-emption of host resources, higher liana loads, and higher liana reproductive output per infested host. If the resulting positive density-dependence, whatever its origins, is sufficiently extreme, it could generate alternative stable states of high and low liana prevalence.

Liana Loss

Countering the gains in newly infested trees due to colonization are losses when infested trees die or lose their lianas (Figs. 1A, 1C). Liana-infested trees can lose their lianas when liana-infested branches are dropped, when lianas are pulled out of the tree or severed by a neighboring branchfall or treefall, or when lianas die due to disease, senescence, or other causes. In the simplest case, the rate at which liana-infested trees lose lianas is assumed to be a constant unrelated to the number of trees infested, so that total fluxes are proportional to the number of trees infested (Fig. 1C). This rate (v in our simple model) depends on liana traits (e.g., climbing strategy), tree traits (e.g., tree architecture), and environmental factors (e.g., windspeed) (Putz 1984a). Hypothesized tree defenses to increase the liana loss rate include higher trunk and branch flexibility, self-pruning of branches and/or large leaves, and bark shedding, although there are few studies testing these ideas (Hegarty 1991).

Alternatively, liana loss rates (per tree) may increase or decrease with the proportion of trees infested. We expect mean liana loads on individual trees to increase with the proportion of trees infested. Higher liana loads on a given branch would be expected to increase branchfall rates and thus loss rates. On the other hand, insofar as higher liana loads are associated with more lianas on a given tree, the probability that a tree entirely loses all its lianas could decrease with increasing liana load. Thus, the total flux of trees from liana-infested to liana-free could increase more than proportionally or less than proportionally with the proportion of trees infested (faster or slower than linear increase in Fig. 1C), thereby altering the equilibrium proportion infested (Fig. 1D).

Host Demography

The literature on variation in the proportion of trees infested with lianas within and among sites has focused on differences in liana colonization and loss (e.g., Putz 1984a). However, host demographic rates also limit the proportion of trees infested with lianas. Most obviously, mortality of infested trees removes infested trees from the community, to be replaced by recruits that are initially liana-free. Thus, the higher the mortality rate of infested trees (α in our simple model), the lower the proportion that will be infested for any given liana colonization and liana loss rates (Visser et al. 2017). The mortality rate of infested trees depends on the environment, tree traits, and liana traits, and increases with liana load (Ingwell et al. 2010, Wright et al. 2015). Thus, insofar as mean liana loads are higher when the proportion of trees infested is higher, we might expect the total mortality of infested trees to rise more than proportionally with the proportion of trees infested with lianas (faster than the linear increase shown in Fig. 1C), thereby decreasing the equilibrium proportion infested (Fig. 1D).

Host demographic rates have additional effects on the proportion of trees infested that are not captured in our simple model. Higher baseline (liana-free) tree mortality rates mean shorter tree lifespans and less time for trees to accumulate lianas before they die, reducing the proportion of trees infested. Negative effects of lianas on tree growth (Clark and Clark 1990, Ingwell et al. 2010) will reduce transitions of liana-infested trees into the larger size classes, and thereby reduce the proportion of large trees that are liana-infested.

Synthesis

Liana colonization, liana loss, and host demography necessarily together determine the proportion of trees infested with lianas (Fig. 1A). A key challenge is to elucidate these rates, their variation with proportion in-

fested (i.e., the shapes of the functions in Figs. 1B, 1C), and the controls on these rates—e.g., determining to what degree the colonization rate is limited by the availability of liana seeds and shoots, understory light, and/or understory vegetation that provides trellises to the canopy. This will then illuminate what factors are most important for determining variation in the proportion of trees infested with lianas among species and sites, as we show in Visser et al. (2018a). Regulation requires negative density-dependence, and an obvious source of negative density-dependence on the proportion of trees infested with lianas is the declining availability of liana-free susceptible host trees. Additional negative density-dependence may emerge if liana loss rates and/or infested tree mortality rates increase with proportion of trees infested, as they may if mean liana load increases in parallel (discussed in the next section). Importantly, there is potential for alternative stable states of high and low liana infestation levels if there is sufficient positive density-dependence in liana colonization pressure, and/or if the liana loss rate declines sufficiently with the proportion infested, as discussed previously.

Liana Load within Individual Trees

A tree's liana load—the mass of lianas within its crown and the amount of light they preempt—affects the contribution that lianas in that tree make to colonizing other trees, the probability the host loses its lianas, and host mortality, growth, and fecundity. Thus, understanding what determines liana load within a host tree is a critical component of understanding what determines liana abundance more generally. Just as the proportion of trees infested with lianas parallels the proportion of hosts infected in disease ecology, so liana load within a tree crown parallels pathogen load within the host. Liana loads can in part be understood in terms of evolution of virulence—that is, selection for lianas with the highest reproductive number, defined as new hosts infested per infested host (Anderson and May 1982). This selection takes place in the context of a fundamental tradeoff between the benefits of higher liana load and associated resource preemption against the cost to the lianas of negative effects this load imposes on its host (Ichihashi and Tateno 2011).

Below, we first consider factors that influence selection on what we call the *target liana load*—that is, the liana load a liana seeks to achieve. In discussing target liana load, we focus on *liana leaf area index (LAI)* within the host crown, defined here as the total leaf area of liana leaves divided by the crown area, although we recognize that there are other aspects of liana load as well. We address three categories of factors shaping target liana load: diminishing returns from additional liana leaves, negative feedbacks

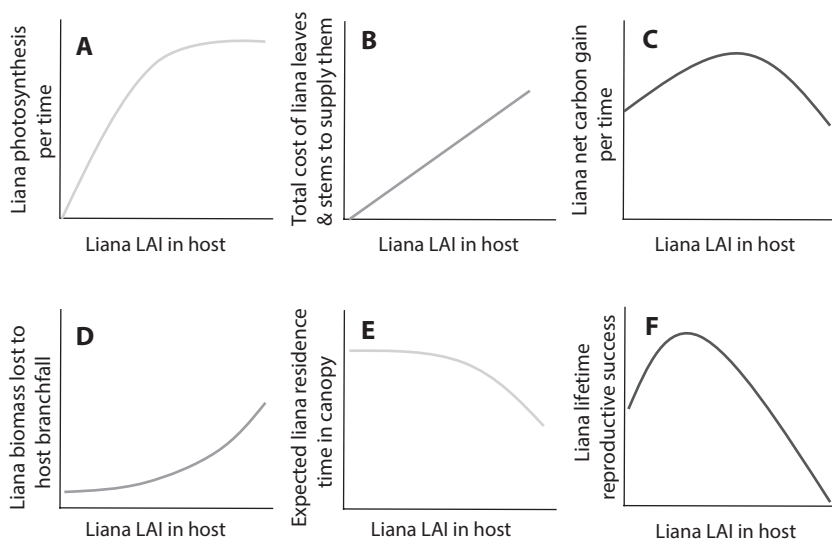


FIGURE 2. The hypothesized change in total benefits (light gray) and costs (dark gray) accruing to lianas within a particular host crown, and net impacts on liana success (black), as a function of the leaf area index (LAI) of lianas within that host crown. Liana LAI is the total liana leaf area on a given host divided by the total host crown area, and is used here as a measure of liana load. (A) Total photosynthesis per time is a saturating function of liana LAI because self-shading causes diminishing returns of additional liana leaves. (B) The total cost of liana leaves and the stems to supply them increases approximately proportionately with liana LAI. (C) Liana net carbon gain per time is a unimodal function of liana LAI, due to the combination of saturating returns and continually increasing costs. (D) Liana biomass losses to host branch fall increase with liana LAI, reflecting negative feedbacks on host tree branch retention. (E) Expected liana residence time in the canopy, and thus liana lifetime sun exposure (light access) and wind exposure (seed dispersal success), all decrease with liana LAI, reflecting negative feedbacks on host survival and growth. (F) Liana lifetime reproductive success is a unimodal function of liana LAI, with a peak at a lower LAI than that which maximizes liana net carbon gain per time (C). All of these curves will vary depending upon liana life history strategies (e.g., aggressive versus conservative, climbing mode), tree life history strategy (e.g., fast versus slow), and the environment. For example, photosynthesis at a given liana LAI (A) will be increased by a longer growing season, higher host light availability, and more aggressive liana leaf placement strategies, whereas the cost per liana LAI (B) will be increased by greater host tree height, and by greater per-height liana stem construction costs due to frost, drought, or a twining climbing strategy. Similarly, liana residence time (E) will be decreased by higher tree mortality rates and more negative effects of lianas on host tree survival.

from burdening host trees, and within-host competition among lianas. We then further consider factors that cause liana loads to be less than the target liana load.

Diminishing Returns of Higher Liana Leaf Area

Lianas, like most plants, tend to place their leaves disproportionately in the greatest-light environments they can reach. As a liana adds more leaves within a given host tree, accessible high-light positions are progressively exhausted, and additional leaves placed in the same crown are relegated to successively lower-light environments. Thus, benefits of additional leaves go down as the number of leaf layers increases, and total carbon gain of lianas on the host tree eventually saturates (Fig. 2A). At the same time, the marginal cost of leaves remains approximately constant, so that the total cost of leaves increases approximately proportionally with liana LAI (Fig. 2A). The combination of diminishing marginal returns and approximately constant marginal costs causes total liana net carbon gain per time to be a unimodal function of liana LAI (Fig. 2C). The diminishing returns of higher liana leaf area within a given crown are qualitatively the same for trees and for lianas. They have the potential to *regulate* liana LAI, just as they regulate tree LAI. We expect lianas to stop making leaves on a given host tree at or below some light level at which additional leaves are no longer a good investment and the total liana net carbon gain per time starts to decrease.

We hypothesize that the marginal costs of additional leaves are higher for climbing plants than for self-supporting trees, even though the total costs of supporting leaves are higher for trees. We thus further hypothesize that the liana LAI that maximizes net carbon gain of a resident liana on a host tree will be lower than the tree LAI that maximizes net carbon gain for the host. Our logic is that the marginal costs of leaves of canopy lianas include not only the costs of the leaves themselves, but also of the plumbing to the ground (xylem, phloem) required to supply these leaves with water and nutrients. In trees, we expect the size of the stem to be determined primarily by structural needs, and to be more than adequate for water and nutrient transport, so that the marginal cost of supplying an additional leaf with water are miniscule. In lianas, in contrast, the size of the stem is determined primarily by transport needs, and thus marginal costs for additional leaves are high, and become ever higher as the canopy becomes taller (and the stem becomes longer). The marginal cost of each additional liana leaf might decrease somewhat with increasing LAI if shade leaves are constructed more cheaply or require less water, but it is nonetheless considerably higher than the marginal cost for a tree. This difference is expected to lead lianas to have higher break-even light levels for

leaf deployment than their host trees, with larger differences for taller hosts. Empirical observations are consistent with the prediction that lianas will have fewer leaf layers than trees. A review by Hegarty and Caballé (1989) found liana LAI of 1 to 3, whereas host tree LAI was 5 or more. This difference in LAI cannot be attributed to inherently lower shade tolerance in lianas: Even in a tropical forest where most canopy lianas have few or no leaves in the shade (Avalos et al. 2007), most liana species build and maintain shade leaves as juveniles in the understory (Gilbert et al. 2006).

Increasing Negative Feedbacks from Burdening the Host Tree

Additional negative density dependence of liana loads arises because higher liana loads impose increasing burdens on the host tree, and negative consequences for the host in turn feed back to resident lianas. First, the greater weight of more liana biomass in the tree increases the probability of branch-fall (Fig. 2D). Liana biomass that was on a branch that falls may be torn to the ground, imposing a cost on the respective liana or lianas. Or, in a best-case scenario for a liana, liana leaves that were on a branch that fell may be left hanging in the air in positions that are less optimal for light interception than those they occupied previously, positions that are likely to lead to dieback and reallocation of liana resources. In the worst scenario for a liana, the liana mass on the falling branch may take the entire liana with it or sever the stem linking the liana in the crown to the soil, removing the liana entirely from that host canopy, and potentially killing it. An increase in branchfall risk with liana load reduces liana residence time in the canopy, and thus expected associated future benefits (Fig. 2E).

More generally, greater liana load on the host tree will increase the mortality risk of the host and decrease its expected future growth, both of which have negative consequences for resident lianas. Most lianas place leaves where they pre-empt light that would otherwise be captured by the host tree, thereby reducing host carbon gain, reducing host growth and reproduction, and increasing host mortality (Visser et al. 2018b). The physical weight of higher liana loads also increases the structural burden on trees and the associated risks of treefall. Tree death in turn removes resident lianas from their advantageous positions in the canopy, whether immediately (treefall) or soon thereafter (standing dead tree) (Fig. 2E). Even if a resident liana survives the death of its host, it has lost or soon loses the scaffolding that provides it with access to light and suffers the consequences. Slowing tree growth has similar, although milder, negative consequences for resident lianas, as it reduces the future area of scaffolding that the resident lianas can benefit from in this host tree and increases the chance that light availability at the host crown will diminish as the host tree is overtopped by

neighbors (Fig. 2F). Less favorable canopy positions also reduce the wind to which lianas are exposed, and thus reduce expected seed dispersal distances of the many lianas that are wind-dispersed (in tropical forests, lianas are considerably more likely to be wind-dispersed than are trees (Muller-Landau and Hardesty 2005)). When these negative feedbacks are taken into account, we expect the reproductive success of a liana on a given host tree will generally be maximized at a liana load that is lower than that which maximizes liana carbon gain per unit time (Ichihashi and Tateno 2011) (Figs. 2C, 2G). This is a classic case under which we expect evolution of reduced virulence in a parasite (Levin and Pimentel 1981, Anderson and May 1982).

It is important to recognize that there need not be a single optimal target liana load for all lianas at a site. Liana species co-occurring at the same site can vary widely in their host exploitation strategies and associated impacts on and feedbacks from host trees, paralleling variation in virulence among microbes co-occurring in the same host population. Such variation may in part arise in response to host heterogeneity, such as variation among co-occurring host tree species in response to liana infestation (Visser et al. 2018b), but can also emerge from game-theoretic dynamics even given homogenous host populations. Ichihashi and Tateno (2011) documented coordinated variation among four co-occurring temperate liana species in leaf light environments and effects on host growth. The most aggressive species placed more than half its leaves in very high-light environments (greater than 80% of full sun) and reduced host growth by 42%; the least aggressive placed 90% of its leaves in very-low-light environments (less than 20% of full sun) and had no effect on host growth; the two other species were intermediate in both respects. The liana species also varied in the number of host trees occupied by a single liana: The least aggressive species always occupied only a single tree, whereas the most aggressive species averaged 3.88 hosts per individual liana, and, of the two intermediate species, one averaged 1.59 and the other 2.56 hosts. A liana species that always occupied only a single tree would be expected to face especially strong negative feedbacks from burdening its host, and to have its interests relatively closely aligned with those of its host, to the point where it may even have an essentially commensal strategy, and an associated low target liana load (Ichihashi and Tateno 2011).

Within-Host Competition among Lianas

The above arguments regarding target liana loads implicitly assume that there is a single liana in any given host, but liana-infested trees often host more than one individual liana. Indeed, in one tropical site, 44% of infested trees hosted more than one *species* of liana (Visser et al. 2018b). Where

there are multiple lianas in a single host, each liana bears the full cost of any restraint in its leaf deployment and proliferation, whereas the benefits of higher host survival and growth may be shared with other resident lianas. This can in principle set the stage for a tragedy of the commons favoring more aggressive host exploitation strategies and higher target liana loads (Nowak and May 1994, Mosquera and Adler 1998). Such dynamics could be mitigated if different lianas occupy different parts of a tree crown, and if feedbacks to branch growth and survival are largely localized. However, in many cases lianas intermingle in the crown. Further, the presence of one liana in a host crown often makes it easier for additional lianas to infest the tree, as the first liana stem can itself provide a route to access the canopy. Overall, it seems highly likely that the potential for within-host competition with other lianas substantially shapes selection on liana strategies, and that it is likely to favor more aggressive strategies.

Underachieving Target Liana Loads

Of course, realized liana loads may often be well below the theoretical target liana loads of the liana or lianas in a given crown. The clearest example of this is the presence of many trees with zero liana loads, which are extremely nonoptimal from the liana's perspective. The same forces that control the proportion of trees infested and lead many trees not to be infested, also contribute to "underinfestation". Most obviously, many trees with low liana loads may have been colonized relatively recently and be on their way to higher liana loads, with that process of liana spreading through the crown taking time.

In other cases, parts of trees may be inaccessible, limiting liana loads within those trees, just as there are some trees that are inaccessible to colonization. For example, if an upper tier of branches is separated from a lower tier by considerable vertical distance and accessible only via a large trunk, then lianas that cannot climb large trunks will be unable spread from the lower tier to the upper tier. Liana physiology may also limit where lianas place their leaves and thus the amount of light that is pre-empted; in particular, some species of lianas can deploy their leaves only close to trunks and major branches (e.g., ivy) (Putz and Holbrook 1991). Finally, mutualists may also play a role in making some areas of trees inaccessible, just as they make some trees inaccessible; for example, mutualist ants of epiphytes restrict liana spread in some emergent trees (Tanaka and Itioka 2011).

Synthesis

There are multiple sources of negative density-dependence that have the potential to regulate liana load within host crowns, by insuring that liana reproductive success declines with increasing liana load above a

certain “target liana load” (Figs. 2C, 2G). This target liana load may vary among liana species, even within the same site, as there may be multiple optimal strategies. Multiple optimal strategies may emerge from variation in other liana traits influencing costs and benefits of different liana loads, from host heterogeneity, and simply from the game-theoretic nature of the underlying problem (Nowak and May 1994). In the end, however, such optimal strategies may or may not be particularly important in any given system, as liana loads may in practice often be well below target liana loads due to limitation by other factors, such as those that limit the proportion of trees infested (see the previous section, Proportion of Trees Infested with Lianas). All else being equal, a higher proportion of trees infested is expected to increase absolute colonization rates, and thereby increase realized liana loads relative to target liana loads, as lianas arrive in trees sooner and have more time to reach their target loads.

Proportion of Landscape in a Liana-Dominated, Low-Canopy State

Finally, at the landscape scale, we can think of areas as being in one of two states: either (1) tree-dominated forest, including tree-dominated canopy gaps, liana-free canopy trees, and liana-infested canopy trees, or (2) liana-dominated gaps, or more generally liana-dominated, low-canopy areas. In many types of forest, the entire area is tree-dominated, with no area in a liana-dominated, low-canopy state. In these landscapes, the liana-dominated low-canopy state must be unattainable and/or unviable (zero rate of transition into this state and/or infinite rate of transition out). In most other forests, liana-dominated gaps are rare, constituting a sort of temporarily arrested succession, into and out of which patches transition (Schnitzer et al. 2000). In the few landscapes in which liana-dominated, low-canopy states constitute a substantial fraction of total area, it appears that transitions between the states continue (Tymen et al. 2016), although there are areas in which the liana-dominated, low-canopy state appears to be highly persistent (Foster et al. 2008).

The frequency of the liana-dominated, low-canopy state at the landscape scale is governed by the rates of transition into and out of this state, and any frequency-dependence in these transitions (Fig. 3). In the simplest case, if the transition rates are density-independent, then there is a single and stable equilibrium proportion of the area expected to be in the liana-dominated, low-canopy state (solid and dashed lines in Figs. 3B–3D). If transitions in both directions are positively frequency-dependent, then alternative stable states are possible (dotted lines in Figs. 3E–3G). Such

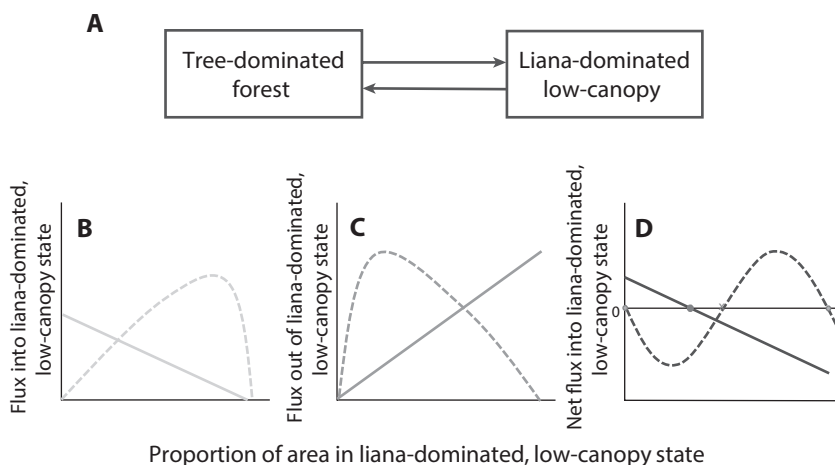


FIGURE 3. (A) The proportion of a landscape that is in a tree-dominated forest relative to the proportion in a liana-dominated, low-canopy state can be explained as a function of the rates of transition between the two, and how these vary with the relative proportions (if they do). Here tree-dominated forest encompasses tree-dominated low-canopy areas as well as areas with large trees, whether those trees are liana-infested or liana-free. (B) If the probability that a tree-dominated patch transitions to liana-dominated, low-canopy state is independent of the frequency of the two types of the landscape, then the flux of such transitions is proportional to the frequency of tree-dominated areas, and declines linearly with the proportion of liana-dominated areas (solid line). Alternatively, the transition rates may be frequency-dependent, reflecting dependence on the availability of seed sources as well, in which case the flux is a unimodal function of the frequency (dashed line). (C) Similarly, transitions out of the liana-dominated low-canopy state increase proportionally with the frequency of such patches if transition probabilities are frequency-independent (solid line), or may be a unimodal function if there is frequency-dependence (dashed line). (D) If neither of the transition probabilities is frequency-dependent (solid lines in (B) and (C)), then the net flux into the liana-dominated, low-canopy state will be a linear decreasing function of the frequency of this state (solid line in (D)), resulting in a stable equilibrium frequency (filled circle), which may be zero. If the transition probabilities are both frequency-dependent (dashed lines in (B) and (C)), then the net flux will be a more complex function of frequency (dashed line) and there may be alternative stable states of low and high frequencies of liana-dominated, low-canopy areas (open circles) as well as an unstable equilibrium x .

positive frequency-dependence is plausible, given that landscape-level abundance of a given vegetation type would be expected to feedback positively on seed availability and juvenile abundance, but has not been established.

A fundamental open question concerns the rates and controls on transitions between tree-dominated forest and liana-dominated low-canopy vegetation. For example, what is it that enables one or more trees to eventually “punch through” the surface of a liana-choked gap and grow to the canopy unencumbered by lianas? Are such escapes disproportionately by tree species with specific adaptations against lianas, such as mutualisms with ants that cut tendrils (Janzen 1969, Fiala et al. 1989)? Or do successful escape events generally follow some dieback of the dominant liana in that area of the gap, perhaps due to disease or senescence? It has been hypothesized that lianas are especially vulnerable to host-specialized natural enemies, perhaps because of their high frequency of vegetative propagation (Gentry 1991a). The dominance of kudzu and some other invasive lianas outside their native ranges—but not within them—is consistent with the idea that natural enemies of lianas likely play an important role in enabling escape from (and/or preventing transitions to) the liana-dominated, low-canopy state. It is also possible that disturbances or unusual environmental conditions are crucial for transitions in one direction or the other. Multiple authors have hypothesized that large patches of liana-dominated forest in South America originated after large-scale disturbance (Webb 1958, Balée and Campbell 1990).

Discussion

Lianas are critically important components of forest ecosystems, whose abundance has major consequences for forest carbon stores and cycling (van der Heijden et al. 2015), and for the relative performance of different tree species (Muller-Landau and Visser 2019). Yet ecologists remain very ignorant of liana strategies and the factors that control the relative abundance of lianas pursuing different strategies, which we argue is critical to understanding the overall abundance and impact of lianas in forests. There are central unanswered questions concerning the determinants of variation in liana abundance at the within-crown, within-forest, and landscape scales. These tie into unanswered questions concerning explanations for empirical variation in liana abundance with climate, forest age, and host tree life history strategy (Schnitzer 2005, DeWalt et al. 2015). The considerations discussed in this essay provide an organizing framework for contrasting hypotheses to explain such spatial variation in liana abundance (Tables 1,2).

Table 1. Consistency between Well-Established Patterns of Variation in Liana Abundance among Forests and Hypothesized Explanatory Mechanisms Motivated by Consideration of the Factors That Limit the Proportion of Trees Infested

		<i>EMPIRICAL PATTERNS</i>		
		<i>TROPICAL FORESTS > TEMPERATE FORESTS (CENTRY 1991A, CENTRY 1991B, SCHNITZER 2005)</i>	<i>EARLY SUCCESSIONAL FORESTS > LATE SUCCESSIONAL FORESTS (DEWALT ET AL. 2000, BARRY ET AL. 2015)</i>	<i>DRY TROPICAL FORESTS > WET TROPICAL FORESTS (SCHNITZER 2005, DEWALT ET AL. 2010, DEWALT ET AL. 2015)</i>
<i>PATTERNS CONSISTENT WITH MECHANISMS?</i>	<i>RELEVANT FIGURE</i>			
Higher densities of small understory trees increase the availability of trellises and thus liana colonization rates (Putz 1984b, Putz and Holbrook 1991, Balfour and Bond 1993).	1B	Yes. Tropical forests have more small understory trees.	Yes. Younger forests have more small understory trees.	Yes. Dry forests have more small understory trees.
Higher understory light levels increase liana juvenile survival and growth, increasing liana colonization rates (Hegarty 1991).	1B	No. Tropical forests have lower understory light availability.	No. Younger forests have lower understory light availability.	Yes. Dry forests have higher understory light availability.
Higher canopy tree mortality rates decrease the proportion of trees infested with lianas.	1C	No. Tropical forests have higher canopy tree mortality.	No. Younger forests have higher canopy tree mortality.	Yes. Dry forests have lower canopy tree mortality.

Hypothesized mechanisms

Table 2. Consistency between Well-Established Patterns of Variation in Liana Abundance among Forests and Hypothesized Explanatory Mechanisms Motivated by Consideration of the Factors That Limit Liana Load

		<i>EMPIRICAL PATTERNS</i>	
		<i>TROPICAL FORESTS > TEMPERATE FORESTS (CENTRY 1991A, GENTRY 1991B, SCHNITZER 2005)</i>	<i>EARLY SUCCESSIONAL FORESTS > LATE SUCCESSIONAL FORESTS (DEWALT ET AL. 2000, BARRY ET AL. 2015)</i>
<i>PATTERNS CONSISTENT WITH MECHANISMS?</i>	<i>RELEVANT FIGURE</i>		<i>DRY TROPICAL FORESTS > WET TROPICAL FORESTS (SCHNITZER 2005, DEWALT ET AL. 2010, DEWALT ET AL. 2015)</i>
Higher solar radiation increases expected carbon gain per leaf, favoring higher liana LAI.	2A	Yes. Tropical forests have higher solar radiation.	Yes. Dry forests have higher solar radiation.
Shorter canopies reduce the costs of supplying liana leaves with water and nutrients, favoring higher liana LAI.	2B	No. Temperate forests are on average shorter.	Yes. Dry forests are shorter.
Seasonal drought or frost increases the cost of supplying liana leaves with water and nutrients, favoring lower liana LAI.	2B	Yes. Temperate forests have seasonal frost.	No. Dry forests have seasonal drought.
Host tree deciduousness enables phenological niche differentiation between lianas and trees, mitigating negative impacts of lianas on hosts, favoring higher liana LAI.	2D,E	No. Temperate forests have more deciduousness.	Yes. Dry forests have more deciduousness.
Higher canopy tree turnover reduces the value of host survival to lianas and thus favors higher liana LAI.	2E	NA. Yes. Early successional forests have higher turnover.	NA.

Hypothesized mechanisms

NA indicates that the hypothesized mechanism is not relevant to that comparison because the relevant factor does not vary strongly and systematically between the forest types being compared.

Globally, forests vary strongly in liana abundance overall and at all three of the scales distinguished here: the proportion of trees infested with lianas, the liana loads of infested trees, and the proportion of the landscape in a liana-dominated, low-canopy state. We suggest that variation in liana abundance can ultimately be explained by variation in the factors that regulate and limit lianas at one or more of these scales, with different factors potentially driving variation along different gradients. Rates of liana colonization, liana loss, and liana-infested tree mortality—which together determine the proportion of trees infested—all vary with the environment, liana species, and tree species (Visser et al. 2018a). Variation in these factors among forests naturally motivates hypotheses to explain variation in the proportion of trees infested with lianas and thus liana abundance, some of which were first advanced decades ago (Table 1). Similarly, the costs and benefits of different liana loads, as well as the degree to which target loads are realized, also vary with the environment, liana species, tree species, and their interaction. Variation in such factors along environmental gradients and between forest types naturally generates additional hypotheses to explain variation in liana loads and thus liana abundance (Table 2). Finally, expected rates of transition into and out of low-canopy, liana-dominated states, also vary strongly among forests and depend on the combination of liana and tree species traits. A better understanding of the controls on these transitions is critical to understanding variation in the frequency of such areas among forests.

Understanding what controls liana abundance is critical not only to understanding geographic variation in liana abundance and forest structure today, but also for predicting how liana abundance will respond to global change—another unanswered question. Liana abundance is increasing in Neotropical forests, and multiple hypotheses have been advanced to explain this pattern (Schnitzer and Bongers 2011). Increasing atmospheric carbon dioxide is hypothesized to favor lianas by increasing the survival and growth of juvenile lianas in the shaded understory (Korner 2009), which would be expected to increase liana colonization rates and thus the proportion of trees that are infested. Another hypothesis suggests climate change may drive increases in liana abundance as increases in evaporative demand from increasing temperatures outstrip increases in rainfall in many tropical areas, effectively making forests drier, consistent with higher liana abundances in drier tropical forests, a pattern that can itself be explained through a number of mechanisms (Schnitzer 2005) (Tables 1 and 2). Higher rates of disturbance, both natural and anthropogenic, also favor lianas as disturbances increase the abundance of early successional forests in which lianas thrive,

and potentially increase transition rates to low-canopy, liana-dominated states. Finally, the introduction of nonnative lianas to areas lacking their natural enemies seems to threaten increased overall liana dominance in areas where these lianas become invasive (e.g., kudzu in the southeastern United States).

We hypothesize that a complete understanding of liana abundance and liana impacts on trees and forest ecosystem properties will require understanding what shapes the functional composition of liana communities. Liana species—even in the same forest—can vary widely in their traits (Asner and Martin 2012, Gallagher and Leishman 2012, Wyka et al. 2013) and host exploitation strategies, with important consequences for host tree growth and survival (Ichihashi and Tateno 2011). This parallels variation in virulence among co-occurring pathogens and parasites, with similar fundamental tradeoffs in which more aggressive resource acquisition by the liana comes at the cost of lower host growth and survival (Mosquera and Adler 1998). Changes in liana loads and liana abundance across sites are accompanied by shifts in the functional composition of liana communities, and specifically in the relative abundance of what might be considered more- versus less-virulent liana strategies. Different environments and tree communities select for different liana strategies and combinations of strategies, with liana communities themselves also shaping tree communities, contributing to a feedback loop. A game-theoretic framework is essential to understanding the liana strategies that emerge in any given forest. Explicit treatment of coinfection and host heterogeneity will also be necessary to understand liana functional composition in many forests. Such a research effort will also yield insights into liana diversity.

Here we have argued that tree–liana interactions can usefully be framed as host–parasite relationships, especially in the context of understanding the proportion of trees infested with lianas. Treating lianas as parasites ties into a large and relevant literature of models and empirical research in host–parasite interactions and disease ecology. However, although a host–parasite framework is broadly useful for understanding lianas, there are also competitive and even mutualistic aspects of the relationships of lianas with trees. Lianas compete with trees belowground for water and nutrients as classic competitors (Stewart and Schnitzer 2017). Many liana species also have free-standing juveniles that compete directly with tree saplings for regeneration opportunities in the understory and in canopy gaps (Schnitzer and Carson 2010, Stewart and Schnitzer 2017). Lianas can also have some positive effects on their hosts. Lianas may increase nutrient availability and soil quality beneath host crowns through the higher quality of their leaf litter, through mutualisms with nitrogen fixers, and

by transporting nutrients from afar (Tang et al. 2012). The higher electrical conductivity of liana stems relative to trees also means that lianas can serve as lightning rods, diverting electrical current and thereby reducing the probability of tree death from a lightning strike (Gora et al. 2017). A full understanding of liana dynamics and abundance may require explicit consideration of these interactions.

Lianas have long fascinated biologists (Darwin 1865), and much has been written on liana physiology, diversity and distribution, and effects on trees and forest ecosystems (Putz and Mooney 1991, Isnard and Silk 2009, Schnitzer et al. 2015). Nonetheless, lianas remain relatively understudied compared to trees, due to their lesser silvicultural importance combined with the difficulty of measuring and modeling them. Simply censusing liana stem diameters requires far more complicated protocols than those for trees (Gerwing et al. 2006, Schnitzer et al. 2008). Further, measurements of stem rooting location and diameter are much less informative about lianas than they are about trees because biomass is less well-related to diameter for lianas (Gehring et al. 2004), and a single liana may extend great distances from its rooting point (Putz 1984b). Fortunately, new technologies make it easier to map lianas at the top of the canopy (Marvin et al. 2016), and to map the three-dimensional structure of the understory and the routes taken by liana stems within those canopies (Calders et al. 2015). Lianas also pose special challenges for modeling; we are not aware of a single published forest model or vegetation model that includes lianas (Verbeeck and Kearsley 2016), despite their known importance for tree recruitment, growth and survival, and forest dynamics. We argue here that many models from disease ecology can usefully be adapted for lianas (as we have shown in Visser et al. 2018a). The development of spatially explicit, individual-based models of forests that include lianas and liana-tree interactions would also aid in tackling questions of the controls on the abundance of lianas pursuing different regeneration and infestation strategies.

We tend to take it for granted that lianas are not more abundant, just as we take it for granted that the world is green. But just as the answer to the question “why is the world green?” is not self-evident, neither is the answer to the question of why lianas aren’t more abundant. Natural history and considerations of basic biology provide us with insights into the processes that may play a role in governing liana abundance, as described in this essay. The key unanswered questions concern the relative roles of different factors within and across scales, and their importance for understanding variation in liana abundance today and in the future.

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