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Blurred Lines between Competition and Parasitism

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Abstract

Accurately describing the ecological relationships between species is more than mere semantics-doing so has profound practical and applied implications, not the least of which is that inaccurate descriptions can lead to fundamentally incorrect predicted outcomes of community composition and functioning. Accurate ecological classifications are particularly important in the context of global change, where species interactions can change rapidly following shifts in species composition. Here, we argue that many common ecological interactions-particularly competition and parasitism-can be easily confused and that we often lack empirical evidence for the full reciprocal interaction among species. To make our case and to propose a theoretical framework for addressing this problem, we use the interactions between lianas and trees, whose outcomes have myriad implications for the ecology and conservation of tropical forests (e.g., Schnitzer et al. 2015).

Keywords

community ecology; competition; parasitism; population ecology; species interactions.

Introduction

Competition for resources, whether matter, energy, space, power, or even computerized information, incites parasitism. Claude Combes, Parasitism, [8]

Determining the exact ecological interactions that occur among organisms is critical for understanding how ecosystems are structured and for predicting how ecosystems will change over time. For example, competitive and parasitic interactions can result in very different long-term community structure and dynamics. Competitors tend to depress each other's population sizes, resulting in population trajectories that grow or shrink depending on the degree of competitive exclusion. Theoretically, competition is a negative–negative interaction among species that can stabilize population sizes and fluctuations, as well as maintain diversity and facilitate co-existence among species (e.g., Tilman [40]). In contrast, parasitism is a positive–negative interaction, and parasites can regulate their hosts, increasing as a function of host density and subsequently suppressing the host population (Anderson & May [2]). The inverse dynamics between parasite and host can manifest as stable cycling when parasites are obligate, because the parasite population will decrease when hosts are rare. However, when parasites are facultative (or when they possess alternative hosts) they can strongly suppress their host population because they are able to parasitize their hosts, but do not depend on them exclusively to maintain their own population (Hatcher & Dunn [13] , Kang & Fewell [18]). Host–parasite interactions can thus result in host and parasite population trajectories that are dynamic and stable, or dynamic but inherently unstable. Accurately describing a relationship as competitive or parasitic (facultative or obligate) is crucial because an incorrect description can lead to fundamentally different predicted outcomes for interacting populations.

Despite clear theoretical differences in the features that define competition and parasitism, such relationships are not always easy to distinguish in nature, and may be frequently misclassified (Thompson [39]). Misclassification of ecological relationships may be particularly true for parasites that do not feed directly on their hosts, but instead parasitize other forms of host energy. Parasites that use host services, for instance, may rely on similar food resources as their host, which can blur the lines between competition and parasitism. The distinction between competition and parasitism may be further blurred because, in both relationships, interacting individuals can simultaneously incur costs and receive benefits. For example, competing species are subject to the costs of limited resources, but may also receive benefits from their neighbors in terms of facilitation, depending on the severity of abiotic conditions (e.g., Wright et al. [45]). Similarly, parasites derive benefits from their hosts but also suffer from host resistance. That is, the attempts of the hosts to eliminate or limit parasitism are often costly to the parasite. Further complicating this scenario is that the strength of these costs and benefits can fluctuate depending on context. In diverse grassland ecosystems, for example, facilitation is strong when abiotic stress is high (i.e., hot and dry conditions), whereas competition dominates under lower stress conditions when plants can better utilize, and thus compete intensely, for resources (Wright et al. [45]). The dominant interaction type (e.g., competition, parasitism, facilitation) ultimately can be distinguished by assessing the long-term net effects of each species on its counterpart (Fig. [NaN]). In this commentary we argue that common ecological interactions, such as competition and parasitism, are easily misclassified, and these errors have important implications for predicting future community composition and stability.

COMPETITION		PARASITISM	
A negative-negative interaction between players arising from their use of similar resources		A positive-negative interaction between players arising from the parasite's use of the host as a resource	
INDIVIDUAL LEVEL	Costs/benefits		Mechanisms to maximize fitness
	Both competitors suffer net costs through competition <ul style="list-style-type: none"> Trees suffer costs when interacting with lianas¹ It is unknown whether lianas suffer costs when interacting with trees 	Hosts suffer net costs, parasites gain net benefits <ul style="list-style-type: none"> Costs to trees depend on the level of liana infestation² Whether lianas benefit through using trees remains unknown 	
POPULATION LEVEL	Temporal dynamics		Distributions
	Either competitor may be excluded through time; coexistence depends on presence of equalizing/stabilizing mechanisms ⁴ <ul style="list-style-type: none"> Little is known about the long-term dynamics between lianas and trees, including instances of exclusion 	Parasites regulate hosts; coexistence depends on factors like host density and parasite virulence ⁵ <ul style="list-style-type: none"> Lianas negatively affect tree population growth⁴, but their capacity to regulate trees is largely unknown 	
COMMUNITY LEVEL	Correlates with diversity		Guild/trophic structure
	Specialization of competitors tends to increase with diversity <ul style="list-style-type: none"> Whether lianas specialize on trees, and whether their specificity increases with tree diversity, is unknown 	Parasite diversity increases with host diversity ¹² <ul style="list-style-type: none"> Liana diversity is higher in tree-fall gaps and following disturbance; increases with free-living diversity have not be explicitly examined.¹³ 	

FIGURE 1. Patterns and impacts of competition and parasitism across ecological scales, including support and unanswered questions for the generalized liana–tree interaction. ¹Kainer et al. (2014); Schnitzer et al. (2014); Alvarez-Cansino et al. (2015); Martinez-Izquierdo et al. (2016). ²In parasitology, this pattern is known as “intensity-dependent pathology” (Bush et al. 1997) and has been observed in trees from Barro Colorado Island (Ingwell et al. 2010). ³Ant symbionts and branch-shedding have been suggested as tree defenses (among others), although evidence for defenses is tenuous (Putz 1984b, Talley et al. 1996, Campenello et al. 2007, Tanaka & Itioka 2011). ⁴Chesson (2000) . ⁵Parasites can cause the extinction of host populations if pathogenicity is high and the parasite has an alternative means of supporting its population (e.g., facultative parasitism or use of a reservoir host). Obligate or host-specific parasites can become extinct if the susceptible host population falls below the minimum threshold for parasite establishment (Hatcher & Dunn 2011). ⁶Visser et al. (in press). ⁷Putz (1984a); Ledo and Schnitzer (2014); Dalling et al. (2012); Schnitzer et al. (2000). ⁸Schnitzer and Carson (2010). ⁹Parasites often have aggregated distributions among their hosts, where some hosts have many parasites, but most have few or none. ¹⁰Ingwell et al. (2010). ¹¹Studies have not directly tested whether lianas show aggregated distributions among their hosts. However, their highly clumped distributions across the landscape (Schnitzer et al. 2012, Ledo & Schnitzer 2014) suggest that some trees possess many lianas while most have few or none. ¹²Known as the “host-diversity-begets-parasite-diversity” hypothesis (Hechinger & Lafferty 2015). ¹³Schnitzer & Bongers (2002).

Lianas: Tree Competitors or Parasites?

A prime example where the lines between parasitism and competition are blurred is that of lianas and trees. Lianas and trees are the dominant and most abundant vascular plant growth forms in most tropical forests, especially in lowland tropical forests (Schnitzer & Bongers [28]). Trees constitute the vast majority of the plant species diversity and aboveground biomass, as well as the bulk of the forest structure. Lianas are also an important component of these ecosystems because they provide substantial diversity, resources, structural complexity, and habitat connectivity, which are exploited by many animal species (e.g., Schnitzer et al. [30]).

Lianas have strong negative consequences for trees by reducing tree recruitment, growth, reproduction, survival, and even diversity, which has been confirmed by numerous experimental studies (Kainer et al. [17], Schnitzer et al. [35], Alvarez-Cansino et al. [1], Martinez-Izquierdo et al. [23]). Although lianas were once referred to as structural parasites of trees (Stevens [36]), they are now almost exclusively considered to be competitors of trees (Schnitzer & Carson [31], van der Heijden et al. [15], Toledo-Aceves [42]). However, little is currently known about the degree to which trees compete with the lianas that inhabit them, and no in situ studies have attempted to experimentally resolve how trees affect lianas (Toledo-Aceves [42]). If competition from trees is minimal and lianas ultimately benefit more than they suffer from trees, then the liana–tree relationship would most accurately be one of parasitism rather than competition (Fig. [NaN]). Because theoretical predictions for interacting species' population sizes and stability rely on the type of interaction they experience (e.g., competition vs. parasitism), distinguishing between these interactions is critical for predicting the long-term changes in tropical tree and liana abundances.

The uncertainty surrounding liana–tree interactions may have arisen from the appearance of competition between these two growth forms. Lianas and trees use the same resources (e.g., light, water, nutrients), and thus many previous studies have regarded them as competitors. Moreover, there is compelling evidence that lianas have negative effects on trees—as one would expect from a strong competitor. For example, there are now dozens of experimental studies that confirm the negative effects of lianas on the growth and survival of tree seedlings, saplings, and adults (Grauel & Putz [12], Schnitzer et al. [33], [35], Schnitzer & Carson [31], Alvarez-Cansino et al. [1], van der Heijden et al. [15], Martinez-Izquierdo et al. [23]). Lianas also dramatically reduce tree reproductive output, thus lowering the fecundity of their host trees (Kainer et al. [17], Garcia-Leon et al. [10]). The overwhelmingly negative effects of lianas on trees results from the ability of lianas to effectively capture both above and belowground resources, which has a decidedly negative effect on coexisting trees (Schnitzer & Bongers [28], Tobin et al. [41], Toledo-Aceves [42]). While there is little doubt that lianas have a net negative effect on trees, it is premature to classify this interaction as competition because it is unclear whether trees have a net negative effect on lianas.

Parasitism has been classically defined as an intimate and durable interaction because parasites live on or within their hosts for an extended period of time (Combes [8]). More rigorous classifications have been described for parasites that feed on their hosts (Lafferty & Kuris [21]) and many plants, like mistletoe (order Santales), fit this classification scheme well since they possess haustoria that tap into and leach resources from the vascular system of their host trees. While lianas do not feed directly on trees, they do coexist with them in an intimate and durable way. The primary parasitic characteristic of lianas is their use of trees as trellises, which enables lianas to ascend to the forest canopy and access light. Climbing host trees goes beyond parasitism of just structure, but is, in effect, the parasitism of all the energy and metabolic processes that produced that structure. Indeed, trees may increase their diameter-to-height ratios to contend with the added weight of lianas (Schnitzer et al. [33]). By using trees for support, lianas themselves are freed from investing in robust support structures and can allocate more carbon directly to gathering energy.

The advantages of a climbing strategy may be paired with relatively few negative consequences arising from tree competition. Lianas incur some costs from their interaction with trees, because the shade that trees create limits recruitment and growth of small lianas in the forest understory (Schnitzer et al. [32]). Lianas may also face costs from traits that have been suggested as tree defenses, such as bark-shedding (Putz [25], Talley et al. [37], Campenello et al. [6]). However, lianas may have additional mechanisms for mitigating these costs. For example, even relatively small lianas (~ 2 cm in diameter) are typically located in the crown of their host tree (Kurzel et al. [20]), where they pre-empt resources and displace their host's leaves (Kira & Ogawa [19], Rodriguez-Ronderos et al. [26]). Lianas appear to deploy the majority of their leaves in full sun, above those of their host's crown, whereas many tree species are adapted to deploy the majority of their leaves in the lower canopy layers (Avalos & Mulkey [3], Rodriguez-Ronderos et al. [26]).

The benefits that lianas receive from their tree hosts could extend beyond physical structure. One of the fundamental stressors for sun-exposed canopy leaves is the hot and dry environment at the top of the forest canopy, which restricts the ability of those leaves to photosynthesize due to high temperature and high levels of water loss. If the massive amount of transpiration from the crown of a host tree lowers the vapor pressure deficit (VPD) experienced by liana leaves located on the top of their host, then lianas could benefit from their tree hosts beyond the use of their physical structure. A large canopy tree in a tropical forest can transpire more than 1150 kg of water per day (Wullschleger et al. [46]), which could dramatically increase the relative humidity of the layer of air located between the tree and lianas leaves, which would reduce VPD and thus water stress for lianas located at the top of the canopy. Furthermore, some liana leaves are located below the crown of their host tree (Rodriguez-Ronderos et al. [26]), and thus may be protected from intense sunlight and high stress by the leaves of their host. The idea that lianas may benefit from their host tree beyond structural support is novel and promising, but remains untested. Nonetheless, the combination of structural support and the potential reduction in VPD and water stress for lianas on host trees could effectively tip the scale toward a parasite–host interaction rather than a competitive interaction.

If lianas are parasites of trees, they are likely facultative rather than obligate parasites. That is, lianas parasitize trees when trees provide a pathway to access more sunlight; however, lianas are also capable of growing and reproducing when trees are absent. This latter trait is well supported by the ability of lianas to rapidly colonize, grow, and reproduce in treefall gaps and pastures, where trees are mostly absent (Putz [24] , Schnitzer et al. [32]). Indeed, most liana species are found growing more abundantly in gaps than in non-gap sites, and gaps appear to provide an important regeneration niche for lianas (Schnitzer & Carson [31] , Dalling et al. [9] , Ledo & Schnitzer [22]). Lianas can also rapidly colonize newly abandoned pastures where tree growth is sparse, and liana density has been found to equal or exceed that of old growth forests within 5 years of pasture abandonment (Barry et al. [4]).

In addition to improving our general understanding of liana–tree interactions, appropriately characterizing the relationship between lianas and trees will allow us to more accurately predict their long-term dynamics. For example, with new insight into their relationship, our attempts to model tree–liana dynamics may shift from competition models to consumer–resource (host–parasite) models (Visser et al. [44]). As such, lianas would experience a sign shift in their quantitative relationship with trees, from a negative competition coefficient to a positive growth term, which may strongly affect their predicted dynamics and alter the stability of equilibrium points. The distinction between facultative and obligate parasitism is also critical for our predictions, particularly in a rapidly changing world. If increasing perturbations lead to an increase in liana density, we would predict an increase in the rate of liana infestation among trees. Because lianas can kill the trees they inhabit, they create more treefall gaps in the forest, which leads to further liana increases (Schnitzer et al. [34] , Ledo & Schnitzer [22]). This positive feedback may lead to a rapid decrease in tree density unless there are other factors that slow the increase in lianas in a density-dependent manner. The increase in lianas at the expense of their tree hosts is consistent with facultative parasitism, and may explain the current increases in lianas and decreases in trees occurring in many Neotropical forests (Schnitzer & Bongers [29] , Schnitzer [27]).

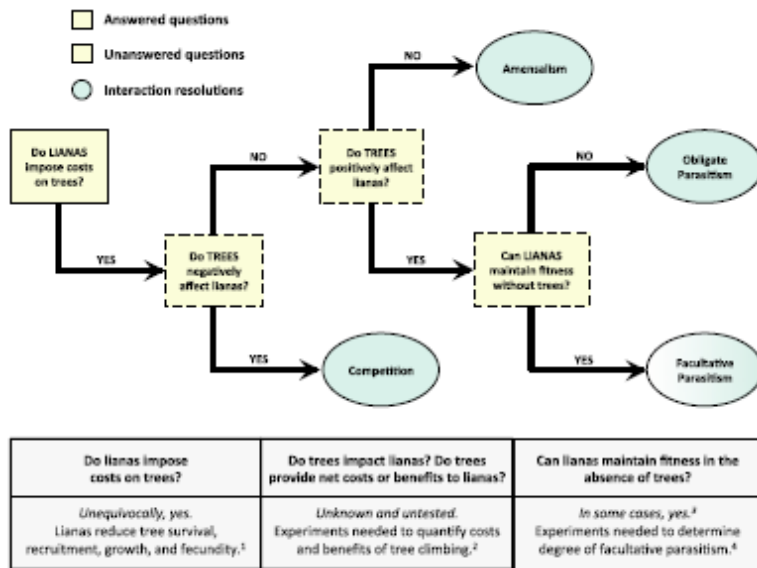


FIGURE 2. Experimental roadmap for determining the true nature of liana–tree interactions. Much of our understanding of liana–tree interactions emerges from studies that focus only on the effects that trees experience (solid line box). However, there are many unaddressed questions (dashed line boxes) that require new and creative experiments to fully resolve this unique relationship. ¹Evidence supporting the general costs lianas impose on trees is overwhelming (Kainer et al. 2014, Schnitzer et al. 2014, Alvarez-Cansino et al. 2015, Martinez-Izquierdo et al. 2016). Future research will benefit from measuring variation in both tree susceptibility and liana pathogenicity. ²No in situ studies have investigated the effects of trees on lianas. This is a critical knowledge gap that can be addressed through field experiments that measure fitness among climbing versus non-climbing lianas, as well as lianas climbing live versus dead tree structure. Creative experiments are needed to tease apart the costs and benefits lianas receive through their interactions with trees. ³Lianas appear to be able to maintain fitness in the absence of trees. Lianas commonly survive in treefall gaps and can dominate gaps for decades (Schnitzer et al. 2000, Tymen et al. 2016). Lianas can also climb suitable structures like walls, buildings, and telephone poles. ⁴Studies on liana fitness in treefall gaps and on inanimate structures will further our understanding of whether lianas are facultative or obligate parasites of trees. Novel experiments are needed to determine their degree of facultative parasitism, that is, the magnitude of the fitness advantage when moving from a free-living to parasitic lifestyle. The greater the fitness advantage, the more dependent lianas are on trees, which is an important factor in determining their future dynamics.

Unblurring the Lines between Competition and Parasitism

The simplest approach to determine whether the relationship between closely interacting species is competitive or parasitic is to measure the reciprocal effects of the species. For the liana–tree example, the experimental removal of lianas from trees has provided strong evidence for the costs that lianas exert on trees (e.g., Tobin et al. [41], Toledo-Aceves [42], Fig. [NaN]). By similarly manipulating trees and lianas, we can determine the costs and benefits that trees provide to lianas (Fig. [NaN]). If trees have no positive or negative effect on lianas, then the relationship would be characterized as an amensalism (Fig. [NaN]). If trees have a net negative effect on liana fitness, then the liana–tree interaction would be best classified as competition (Fig. [NaN]). In contrast, if trees have a net positive effect on liana fitness by providing structure and potential additional benefits, then the interaction would be parasitism, which could be further distinguished as facultative or obligate (Fig. [NaN]). Determining the degree of facultative parasitism (i.e., the magnitude of the fitness benefit for free-living vs. parasitic lianas) is an important goal for advancing our understanding of how dependent lianas are upon tree populations. Both lianas and trees represent diverse and polyphyletic growth forms (Gianoli [11]), and interaction types and strengths may vary depending on the species pairing. Nonetheless, examining the interactions between these two important growth forms will provide insight into the general nature of the

liana–tree interaction and will provide testable hypotheses for why lianas, as a group, are increasing in density and biomass in many Neotropical forests. Determining the exact nature of species, guild, and growth form interactions may help to explain contemporary changes in tropical forests and is essential for formulating educated predictions for the future of tropical ecosystems.

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