Chapter 21
Functional Roles of Lianas for Forest Canopy Animals

Stephen P. Yanoviak and Stefan A. Schnitzer

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Bullet Points

1. Lianas provide nutritional and structural resources for consumers and are a key source of physical connectivity within the canopy.
2. Ongoing experiments in Panama suggest that physical connectivity is an important determinant of local arboreal ant species richness.
3. Understanding the functional ecology of lianas in the canopy will provide a basis for predicting the broader effects of increasing liana abundance.

Summary

Lianas (woody vines) are key components of tropical forest canopies. They represent a large fraction of total stem density and upper canopy foliage, and have important effects on forest dynamics. Liana abundance is increasing in neotropical forests, which could have far-reaching community- and ecosystem-level effects. Accurately predicting the consequences of this change depends on a clear understanding of the functional roles of lianas. Clearly lianas are detrimental to tropical trees via mechanical loading and competition, but less is known regarding their effects on arthropod

S.P. Yanoviak (✉)
Department of Biology, University of Louisville, Louisville, KY 40292, USA
e-mail: steve.yanoviak@louisville.edu

S.A. Schnitzer
Department of Biological Sciences, University of Wisconsin – Milwaukee, Milwaukee, WI 53201, USA
e-mail: S1@uwm.edu

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diversity in the canopy. This chapter briefly reviews the functional ecology of lianas and summarizes evidence that the inter-tree physical connectivity provided by lianas is an important determinant of local canopy ant diversity. Quantifying ecological associations between lianas and other canopy inhabitants is essential for understanding how ongoing changes in forest structure will affect tropical forest canopy biodiversity, and community and ecosystem processes.

1 Introduction

Lianas are climbing plants with relatively long, slender, woody stems rooted in soil and extending to the forest canopy, where they produce abundant foliage. Like "tree" or "shrub," "liana" refers to a polyphyletic functional group that exhibits considerable structural diversity among taxa (Schnitzer and Bongers 2002). Hundreds of species of lianas exist worldwide, and the liana growth form is represented in nearly all major plant families (Putz and Mooney 1991).

Lianas are among the most conspicuous structural elements of tropical forests. Mature individuals range in length from a few meters to more than half a kilometer and in diameter from a few millimeters to more than half a meter. In lowland tropical forests, lianas commonly represent > 25 % of the rooted woody stems, 35 % of the woody species, and up to 40 % of the foliage area of the upper canopy (Putz and Mooney 1991; Schnitzer and Bongers 2002; Schnitzer et al. 2012). Recent and ongoing studies indicate that liana abundance is increasing in neotropical forests due to multiple, potentially interrelated factors that are partly associated with climatic change (Schnitzer and Bongers 2011; Schnitzer et al. 2011). Consequently, lianas are rapidly emerging as key elements of present and future forest dynamics (Schnitzer et al. 2014).

2 Functional Roles of Lianas

The large, rapidly expanding literature regarding the biology of lianas and their ecological relevance in forest ecosystems is comprehensively reviewed elsewhere (Putz and Mooney 1991; Schnitzer et al. 2014). Briefly, lianas are agents of tree mortality; they influence forest dynamics and patterns of forest regeneration via competition and mechanical parasitism on trees (Schnitzer and Bongers 2002, 2011). At the ecosystem scale, lianas affect gross transpiration rates, forest productivity, and carbon budgets (Schnitzer and Bongers 2002, 2011). Whereas most studies view the functional roles of lianas in forests from the perspective of their conspicuous negative effects on trees, lianas also provide important resources for animals and likely play a role in shaping the evolution of arboreal lifestyles

(Emmons and Gentry 1983; Kilgore et al. 2010). However, very little information exists concerning interactions between lianas and animals.

2.1 Lianas as Food

Liana foliage is an important food source for large herbivores in forest canopies (e.g., Dunn et al. 2012), and the seeds and fruits of some taxa (e.g., *Tontelea, Strychnos*) are opportunistically consumed by primates and other vertebrates both in the canopy and on the ground (e.g., Croat 1978). In contrast, information regarding herbivory and frugivory on lianas by arthropods is relatively limited. This is a significant gap in our understanding of trophic dynamics in tropical forests, given that arthropods are the most diverse and widespread herbivores in tropical forests (Basset et al. 2012). The best studied examples of arthropod herbivory on lianas include *Heliconius* butterflies feeding on *Passiflora* and ithomiine butterflies feeding on lianas in the family Solanaceae (see Ødegaard 2000 and references therein). Arthropod inventories conducted at various tropical locations provide strong correlative evidence that lianas partly determine local arthropod community structure in forest canopies (e.g., Dial et al. 2006). The mechanisms for this pattern remain largely unexplored, with the exception of Ødegaard's (2000) results showing that host specificity for lianas among phytophagous beetles increases local species richness in Panama.

Apart from leaf, fruit, and seed resources, lianas also provide pollen, nectar, and extrafloral nectar that are attractive to a broad range of consumers. Extrafloral nectar is a particularly important food source for aggressive, behaviorally dominant arboreal ants, and the distribution of carbohydrates derived from lianas and their herbivores may determine local ant community structure (reviewed in Rico-Gray and Oliveira 2007). Despite a wealth of literature pertaining to ant-plant associations and ant ecology in general (e.g., Hölldobler and Wilson 1990), many fundamental questions regarding ant-liana trophic interactions remain unanswered.

2.2 Lianas as Structure

Lianas contribute to the structural heterogeneity of tropical forests and expand the availability of physical resources for animals. Specifically, liana foliage provides shelter for a wide range of arboreal taxa, liana stems provide perches and grips for volant and brachiating species, and all liana surfaces provide foraging substrates for insect gleaners. The ecological importance of these functional contributions is revealed by differences in vertebrate assemblages between forests with and without abundant lianas (e.g., Emmons and Gentry 1983). Structural contributions of lianas appear to be particularly important to the maintenance of understory bird diversity and are likely to facilitate the presence of phyllostomids and other bats that feed by gleaning.

Many of the nutritional and structural resources described above are also provided by trees and epiphytes, but lianas are the only source of widespread, persistent connections between tree crowns in the forest canopy. Despite the complex, highly interconnected appearance of tropical forest canopies, continuous physical contact between leaves and branches of neighboring canopy trees is rare. Trees generally maintain a narrow, leaf-free gap between neighboring crowns, commonly called "crown shyness" (Ng 1977). Crown shyness is most evident in even-aged monotypic stands, but is equally common in dense primary forest. The connectivity provided by lianas overcomes crown shyness and influences the foraging activities and general mobility of nonvolant canopy animals, including mammals (Emmons and Gentry 1983). As with many other aspects of forest structure, measuring connectivity is logistically and quantitatively challenging. However, advances in remote-sensing technology (e.g., LiDAR) are quickly making such measurements feasible at ecologically relevant scales.

2.3 Lianas and Canopy Ants

Among invertebrates, ants are the most conspicuous users of liana structure; they commonly incorporate lianas into their foraging trails (Clay et al. 2010; Yanoviak et al. 2012) and often nest in hollow liana stems (e.g., Ward 1989). Some Asian and African ants have quasi-mutualistic associations with lianas, including *Cladomyrma* on *Spatholobus* and *Tetraponera* on *Vitex* (Djiéto-Lordon et al. 2005). In contrast, occupancy of lianas by neotropical twig-nesting ants appears to be entirely opportunistic. Foraging ants may preferentially use lianas to access patchy resources (Clay et al. 2010), and field observations suggest that the narrow, often smooth structure of liana stems enhances ant locomotion and predator avoidance relative to tree surfaces (Yanoviak, unpublished).

Inter-crown connectivity should be particularly important to arboreal ants. In the absence of lianas, access to resources in multiple tree crowns can only be accomplished by descending to the forest floor and traversing the leaf litter, which is hazardous and inefficient (e.g., Yanoviak et al. 2011). Thus, the connectivity provided by lianas is likely to be a key structural resource for ants. We are testing this hypothesis via a large, ongoing liana removal experiment in Panama. We surveyed canopy ants in sixteen 80×80 m experimental plots before and after liana extermination, then added structural connectivity in the form of used climbing ropes suspended between tree crowns. Ants began using the added connectivity almost immediately (Fig. 21.1). Preliminary results show that liana removal reduced average ant species richness in tree crowns by 22 % relative to controls (i.e., plots with intact lianas). The addition of connectivity partly counteracted this effect and increased local (per tree) ant species richness in control plots by ca. 25 %. Collectively, these results indicate that the physical connectivity provided by lianas is an important determinant of local ant diversity in the canopy. Our ongoing studies are exploring the mechanisms for these patterns.

Fig. 21.1 A worker ant, *Camponotus senex*, uses an artificial connection (old climbing rope) to travel between isolated tree crowns. (Photo by S.P. Yanoviak)

3 Conclusions

Increased liana abundance (Schnitzer and Bongers 2011) is one of many factors that will affect the structure of tropical forests over the next few decades (e.g., Wright 2005). Predicting the effects of such changes on forest ecosystems requires a clear understanding of the specific contributions of lianas to canopy biodiversity and other ecological parameters. Lianas are functionally redundant with trees and epiphytes in some respects, but their ecological role as inter-tree connectors clearly distinguishes them from other canopy components. Preliminary results from large-scale experiments show that connectivity is a key resource for small, cursorial organisms like arboreal ants. Similar studies are needed to determine the specific contributions of lianas to the diversity of other major taxa, especially arboreal vertebrates and herbivorous arthropods.

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