Chapter 24

EFFECTS OF LIANAS ON CANOPY ARTHROPOD COMMUNITY STRUCTURE

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OVERVIEW

This chapter reviews the known ecological associations between lianas and arboreal arthropods in tropical forests, and summarizes ongoing work focusing specifically on the ecological connections between lianas and arboreal ants. Lianas are abundant, conspicuous structural components of tropical forests, yet we know relatively little about their effects on local arthropod communities. Inventories of herbivorous taxa and their host specificity in tropical forest canopies show that lianas are significant contributors to local arthropod diversity via bottom-up effects. Ant associations with lianas generally are opportunistic; highly coevolved ant-liana relationships are rare, perhaps due to the greater longevity of arboreal ant colonies relative to liana life spans. Nonetheless, lianas provide important resources for canopy ants, especially physical connectivity and nutrients such as extrafloral nectar. From the perspective of arthropods, lianas are ecologically redundant with trees and epiphytes in many ways; however, only lianas provide persistent physical connections between tree crowns, which function as efficient pathways to distant resources for ants and other cursorial organisms. Preliminary results from a large-scale experiment in Panama show that liana removal decreases local canopy ant diversity, increases Azteca nest density, and alters ant species composition. Given that liana abundance is increasing in tropical forests, understanding their potential role as determinants of local species richness is essential for predicting future patterns of biodiversity more generally in tropical forest canopies.

INTRODUCTION: LIANAS AS A KEY STRUCTURAL ELEMENT OF TROPICAL FORESTS

The relationship between habitat structure and diversity depends on how organisms perceive and use their physical surroundings (Dean & Connell 1987; Bell et al. 1991; Tews et al. 2004). Terrestrial habitat structure largely is defined by vegetation physiognomy (Kenoyer 1929), and variation in vegetation characteristics within and among forests affects the diversity and distribution of both vertebrates and invertebrates (e.g., James & Wamer 1982; Fonseca 1989, Halaj et al. 1998, 2000). Although structure-diversity patterns are supported by observational and experimental data, the effects of individual forest components specifically on arthropod communities are poorly known. For example, the importance of plant architectural diversity (e.g., Lawton 1983), and foliage density and diversity on arthropod community parameters, remain largely undocumented. Such information is ecologically relevant and increasingly important given that disturbance and changing climatic conditions are unlikely to affect all forest components equally (e.g., Dale et al. 2001; Körner 2009).

By first-order approximation, tropical forests consist of four conspicuous living structural elements—trees, shrubs, lianas, and epiphytes—each with very different autecology and consumer faunas (Ødegaard 2000a). Lianas in particular are a key component of lowland forest ecosystems (Gentry & Dodson 1987; Gentry 1991; DeWalt et al., Chapter 11 in this volume). They provide diverse resources for numerous animal taxa (Gentry 1991; Yanoviak & Schnitzer 2013; Schnitzer et al., Chapter 1 this volume) and likely influence the evolution of arboreal animal morphology and behavior (Benson et al. 1975; Emmons & Gentry 1983). Moreover, liana abundance is increasing in neotropical forests due to climatic change, disturbance, and related factors (Phillips et al. 2002; Wright et al. 2004; Ingwell et al. 2010; Schnitzer & Bongers 2011; Schnitzer et al. 2011, 2012; Schnitzer, Chapter 30 in this volume). Thus, understanding the relationships between liana ecology and consumer diversity is essential for predicting patterns of biodiversity in tropical forests over the next century.

ARTHROPOD DIVERSITY IN THE TROPICAL FOREST CANOPY

Tropical rain forest canopies around the world are known for their high arthropod species richness (e.g., Erwin 1982; Stork et al. 1997; Basset et al. 2003; Ozanne et al. 2003; Basset et al. 2012). Many mechanisms have been proposed to explain patterns of arthropod diversity within and among tree crowns (Erwin 1982; Basset 1992b), but few have been adequately tested, in part because experimental manipulations in the canopy are logistically very difficult at ecologically relevant scales. Moreover, accurately estimating arboreal arthropod diversity in the canopy continues to be very challenging despite
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the development and application of diverse sampling methods (Basset et al. 2012; Lowman et al. 2012).

Although patterns of canopy arthropod diversity are difficult to quantify, the collective results of descriptive studies reveal some generalities. For example, arboreal arthropod diversity tends to be vertically stratified, such that more species occur in upper canopy vegetation than in lower forest levels (e.g., Elton 1973; Sutton et al. 1983; Basset et al. 1992, 2001; Su & Woods 2001). There are some notable exceptions to this pattern: tropical ant diversity is lower in the canopy than the litter (e.g., Yanoviak & Kaspari 2000), the abundance and diversity of cloud forest spiders are lower in the canopy than the understory (Yanoviak et al. 2003a), and the species richness of arthropods inhabiting water-filled tree holes tends to decline from the understory to the canopy (Yanoviak 1999). It is also generally evident that host tree specificity is low among canopy arthropods (Stork 1987; Basset 1992a; Basset et al. 1996; reviewed in Ødegaard 2000a), and that patchy microhabitats within forest canopies harbor a large fraction of local arthropod diversity (e.g., Yanoviak 2001; Ellwood et al. 2002; Yanoviak et al. 2003b, 2004, 2006). Finally, canopy arthropod diversity tends to be higher in primary forest than in secondary forest (e.g., Floren & Linsenmair 1999; Schonberg et al. 2004; Floren & Deeleman-Reinhold 2005; Klimes et al. 2012), which may seem intuitive, but is not true for all animal taxa (e.g., Fonseca 1989; Yanoviak et al. 2003a).

Whereas these and other patterns are relatively well established in the literature, many fundamental questions regarding arboreal arthropod ecology remain unanswered. For example, what are the relative contributions of local and regional processes in structuring canopy communities? How important is habitat structure (i.e., physical complexity) to the maintenance of diversity? And, is there correspondence between the distribution of plant traits (nutritional, phenological, etc.) and trait distributions within their arthropod communities (e.g., Basset 1991a, 1992b; Ødegaard 2000a; Yanoviak et al. 2004; Tanaka et al. 2010)? We can begin to address such questions by comparing the fauna of trees with and without specific components, such as lianas (this chapter), epiphytes (Yanoviak et al. 2011a), or young foliage (Basset 1991b). However, controlled experiments involving appropriate focal taxa and distinct structural elements are required to unambiguously separate the effects of physical habitat from nutritional and other contributions of individual vegetation components. Tropical arboreal arthropods and lianas collectively provide an excellent model for such investigations.

ECOLOGICAL ASSOCIATIONS BETWEEN ARTHROPODS AND LIANAS

Given that arthropods and the liana growth form have coexisted for millions of years (Stein et al. 2012), it is likely that some close ecological associations occur between them. If so, it is also likely that trees with lianas support more arthropod species than trees lacking lianas. Despite the large number of faunal inventories that have been conducted in tropical forest canopies, none explicitly addresses this assumption, though some studies do indicate that lianas broadly influence arthropod community parameters (i.e., species richness, abundance, and composition). For example, Stork (1987) showed that the local abundance of lianas (and epiphytes) was more important than tree identity in determining arthropod faunal similarity among trees in Borneo. In an Australian subtropical montane forest, Walter et al. (1994) recorded mite densities >10,600 m$^{-2}$ on liana foliage, which greatly exceeded densities observed on other canopy plants at the site. Likewise, arthropod abundance increased with liana foliage abundance in a dipterocarp forest (Dial et al. 2006), though the type of foliage (tree or liana) ultimately was less important than leaf vs. wood as a determinant of arthropod abundance (Dial et al. 2006). Faunal inventories such as these require enormous amounts of time and effort, and their results, though often correlative or anecdotal, provide a solid foundation for subsequent comparative and mechanistic studies. For practical and ecological reasons, most such studies have focused on herbivores and ants.

Herbivory is ubiquitous in tropical forests (Coley & Barone 1996), and specific contributions of lianas to arthropod community structure in the canopy should be most apparent in herbivorous species. Indeed, the best-known liana–arthropod associations involve highly specialized plant feeders. Commonly observed examples include Heliconius butterflies on Passiflora (Benson et al. 1975; Smiley 1987), Solanaceae-feeding Ithomiinae butterflies (e.g., Trigo & Motta 1990), and
Hylaeogena beetles on Bignoniaceae. In a broad study of liana–herbivore associations, Ødegaard (2000b) found that 24% of ca. 700 species of arboreal phytophagous beetles were associated with both lianas and trees in Panama. Although cumulative species richness was similar between trees and lianas, the number of beetle species specializing on green vs. woody tissues was higher on lianas, whereas the opposite was true on trees. Consequently, only 11% of species in the green tissue feeding guild were shared between trees and lianas (Ødegaard 2000b). Collectively, these results demonstrate that the presence of lianas significantly increases local arthropod diversity in the forest canopy via bottom-up effects. Wolda’s (1979) observations for herbivorous, canopy-dwelling insects in Panama also support this conclusion. Specifically, the abundance and diversity of hemipterans in light trap samples increased with the number of vines in individual Luehea trees (Wolda 1979).

Elevated arthropod diversity in the presence of lianas apparently is a consequence of the relatively high production of new foliage (and tendrils) in lianas compared to trees (Wolda 1979; Hegarty & Caballé 1991; Ødegaard 2000b). Given that tropical plants often trade strong herbivore defense for rapid growth (Coley & Barone 1996; Stamp 2003), and that this trade-off is particularly strong for lianas (Asner & Martin, Chapter 21 in this volume), lianas should support more generalist herbivore species than trees based on their greater relative production of green tissue. Ødegaard’s (2000b) results show the opposite pattern – more green-tissue specialists occurred on lianas than on trees in Panama – suggesting that lianas have stronger herbivore defenses (consequently excluding many generalist feeders) than do trees (Hegarty et al. 1991). The distribution of chemical defenses in a broad range of extant plant taxa (Hegarty et al. 1991), and specific comparisons between trees and lianas (Asner & Martin 2012; Asner & Martin, Chapter 21 in this volume), do not support this hypothesis. Nonetheless, the pattern may have been more prominent in ancient forests: Carboniferous fossils show that lianescent ferns were especially well defended against herbivorous arthropods (Krings et al. 2002). The conflicting results of these studies illustrate the need for more research on the ecology and evolution of herbivory specifically on lianas. To date, most studies addressing liana–arthropod associations and related questions have focused on ants, as discussed below.

### ARBOREAL ANTS IN TROPICAL FORESTS

Ants are an excellent focal taxon for investigations of plant–animal relationships in tropical forests. They are both tractable for field research and relevant to understanding the functioning of tropical rain forests at the ecosystem level. They span approximately four orders of magnitude in body size (Kaspari & Weiser 1999) and play important roles in a wide range of ecological processes (e.g., seed dispersal, soil turnover, and nutrient cycling; Hölldobler & Wilson 1990; Lach et al. 2010). Ants are relatively easy to observe and collect (Bestelmeyer et al. 2000), their taxonomic composition and diversity can be determined without destroying entire colonies (Kaspari 2000), and species-level identifications are possible within many genera (e.g., Longino 2003; Wilson 2003). Moreover, molecularly based ant phylogeny is available to facilitate the interpretation of ecological results in an evolutionary context (Moreau & Bell 2013 and references therein). Finally, ants are particularly relevant to understanding forest canopy ecology because they represent a large fraction of arthropod abundance and consumer biomass specifically in tropical tree crowns (reviewed by Rico-Gray & Oliveira 2007).

Tropical canopy ants and litter ants form distinct communities (Yanoviak & Kaspari 2000), though arboreal ants (i.e., species nesting in aboveground vegetation) will occasionally forage in the understory (e.g., Hahn & Wheeler 2002), and some ground-nesting taxa forage in the canopy (e.g., Atta spp., Paraponera clavata, G. destructor). Many canopy ant species function as secondary herbivores, feeding on the honeydew provided by plant-sucking Hemiptera (Davidson et al. 2003), and thus are protein-limited relative to leaf litter ants (Davidson 1997; Yanoviak & Kaspari 2000; Davidson et al. 2007). Physical aspects of the canopy also uniquely shape the behavior and ecology of arboreal ants. Specifically, canopy ants live in a relatively sunny environment, forage along relatively permanent but highly exposed linear networks, and must cope with the hazard of falling (e.g., Yanoviak et al. 2005, 2011b). Whereas arboreal ants have traits that match these circumstances, not all species are found in all trees, and their distributions are likely determined by local processes such as niche determinism and competition.

It is widely accepted that ants compete for patchy resources (e.g., Hölldobler & Wilson 1990; Davidson...
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1998; Adler et al. 2007; Lach et al. 2010). Aggressive interspecific interactions among ants are readily observed at baits, and resource limitation likely promotes parabiosis (nest sharing; e.g., Longino 2003; Menzel et al. 2008) and trail parasitism (the use of foraging trails, and consequently food resources, by unrelated workers; Adams 1990). Competition among canopy ants often results in mosaic-like species distributions in plantations and forests having relatively low structural heterogeneity (Leston 1978; Adams 1994; Dejean et al. 2007). Such patterns tend to be diffuse or nonexistent among trees in complex and highly connected primary forests (Floren & Linsenmair 2000; Stuntz et al. 2003; Sanders et al. 2007; Klimes et al. 2012; but see Davidson et al. 2007). Likewise, tests of relationships specifically between vegetation structure and ant diversity have given mixed results; arboreal ant diversity increased with tree diversity (a surrogate for structural heterogeneity) in Brazilian savanna forest (Ribas et al. 2003), but decreased with habitat complexity in Australian woodlands (Lassau & Hochuli 2004), and showed no association with epiphyte abundance in trees of Panama (Stuntz et al. 2003).

Despite growing knowledge about the ecology of tropical arboreal ants, a unified framework for predicting local ant species richness and composition (i.e., in individual trees) is lacking. However, progress on this front is emerging; recent observational studies have added to our knowledge of ant species diversity and coexistence in individual trees. For example, comprehensive surveys of felled trees in New Guinea showed that habitat structure (tree density and tree size) is a stronger determinant of local ant species richness than is tree diversity (Klimes et al. 2012). Similarly, resident ants of individual Bornean trees appear to be spatially partitioned by micro-environmental heterogeneity associated with structural complexity (Tanaka et al. 2010). In the Atlantic Forest of Brazil, higher ant diversity in larger individuals of the tree Anadenanthera macrocarpa was attributed to ontogenic changes in tree architecture, which presumably influenced microclimate and the availability of nest and food resources (Campos et al. 2006). Studies of arboreal ants in Brazilian savanna forest suggest that structural variables such as tree size, tree density, and availability of appropriate nest sites are important determinants of diversity (Ribas et al. 2003; Powell et al. 2011). Collectively, these studies indicate that niche determination mediated by habitat structure affects local arboreal ant diversity in tropical forests. Thus, variation in forest components like lianas should have predictable effects on ant communities. Almost all studies of arboreal ant ecology in lowland wet forests note the importance of lianas, but specific contributions of lianas to ant diversity have never been quantified.

ECOLOGICAL ASSOCIATIONS BETWEEN ANTS AND LIANAS

The evolutionary history of ants is closely associated with the diversification of angiosperms (Moreau et al. 2006), and ecological links between ants and tropical trees and epiphytes are common (e.g., Janzen 1966; Beattie 1985; Huxley & Cutler 1991; Dejean et al. 1995; Ellwood et al. 2002; Stuntz et al. 2003; Djieto-Lordon et al. 2004; Frederickson & Gordon 2007). In contrast, coevolved (e.g., mutualistic) associations specifically between lianas and ants are rare (Moog et al. 2003; Djieto-Lordon et al. 2005; Rico-Gray & Oliveira 2007). Climbing plants were abundant in ancient forests during the diversification of ants (Stein et al. 2012; Burnham, Chapter 5 in this volume), and use of liana extralorral nectar is widespread among canopy ants (Bentley 1981; Blüthgen et al. 2000). However, the only examples of tight myrmecophytic associations are the defense of Spatholobus and other lianas by Cladomyrma spp. in Asia (Maschwitz et al. 1989; Moog et al. 1997, 2003; Moog 2009) and Tetraponera tessmanni inhabiting Vitex thyrsiflora in Africa (Djieto-Lordon et al. 2005). In both cases, cavities in the plants created or maintained by the dominant ants also are occasionally occupied by other arboreal ant species. Similarly close associations between ants and lianas are unknown in the neotropics.

The low frequency of conspicuous coevolved associations between lianas and ants may be due to the high turnover rates of lianas relative to other forest components (e.g., Phillips et al. 2005; Ingwell et al. 2010). Few long-term life-history data exist specifically for tropical ants, but colonies of some ant species persist for decades (Keller 1998), and repeated surveys of individual mature trees in Panama over the past 15 years show that most arboreal ant species have long colony longevity (Yanoviak, pers. obs.). A long lifespan in combination with nest site limitation (Carroll 1979; Philpott & Foster 2005) places considerable selection pressure on arboreal ants that use plant cavities for nest sites (i.e., those that do not construct nests of
leaves or carton). Specifically, selection should favor colonization of the most persistent substrates (e.g., trees and shrubs), or the subdivision of nests (i.e., polydomy) among unitary substrates that are short-lived but locally abundant (e.g., dead hollow twigs, live domatia, and epiphytes). Lianas do not neatly fit either scenario due to their patchy distribution and relatively high turnover rates. Also, domatia-like structures appear to be uncommon in the live stems of lianas. Thus, opportunistic use of lianas by ants is likely to be favored over obligate occupancy. This appears to be true within the predominantly arboreal genus *Pseudomyrmex*, which includes many myrmecophytic species, but none that is associated with lianas apart from opportunistic nesting in dead stems (Ward 1989, 1991, 1999).

In contrast to the rarity of mutualisms between lianas and ants, antagonistic interactions between ants and lianas may be quite common. Many neotropical plant-ants (e.g., *Pseudomyrmex* and *Myrmelachista*) maintain their hosts free of vines and other potential competitors by pruning or killing intruders (Janzen 1966; Frederickson & Gordon 2007). Although the best examples of this behavior involve understory trees and shrubs, Tanaka and Itioka (2011) showed experimentally that *Crematogaster difformis* ants exclude lianas from certain emergent trees in Borneo. Presumably the *Pseudomyrmex* ants inhabiting mature *Tachigali* and *Triplaris* spp. trees in the Amazon (Ward 1999) also actively prevent colonization of their hosts by lianas, though this has not been studied. Arboreal ants will wage prolonged attacks on any foreign objects secured to branches within their foraging territories, suggesting that even non-mutualistic canopy ants influence colonization of their home trees by lianas.

Regardless of the nature of the liana–ant associations, lianas provide essential resources that are likely to enhance the local species richness of arboreal ants under most circumstances, especially physical connectivity, nutrients, and low-resistance pathways. Physical connectivity is a key feature of habitat structure at multiple scales, influencing the outcome of local interspecific interactions (Huffaker 1958; Davidson et al. 1988) and ecosystem processes across fragmented landscapes (e.g., Rosenberg et al. 1997, Fischer & Lindenmayer 2007). Physical connections in tropical forest canopies likely play a similarly important mechanistic role in ant species coexistence, though this has never been examined experimentally on a large scale (but see e.g., Davidson et al. 1988, Powell et al. 2011). Despite the high vegetation density of lowland tropical forests, the leaves and branches of neighboring canopy trees almost never have persistent physical contact with each other (commonly referred to as crown shyness: Ng 1977; Putz et al. 1984; Richards 1996). Consequently, in the absence of lianas or similar connectors (e.g., Snaddon et al. 2012), ants nesting in a given tree crown cannot access resources in nearby trees without first descending to the understory and traversing the leaf litter. This exposes workers to predator pressure on the ground between trees, and reduces foraging efficiency due to the increased distance to resources (Weber 1957; Catling 1997; Yanoviak et al. 2011b). Physical isolation of tree crowns also may enhance the local competitive effects of aggressive resident ants such as *Azteca* (Catling 1997). Lianas solve the crown shyness problem for ants and other arboreal animals by forming bridges between neighboring trees (e.g., Koenig et al. 2007; Tanaka et al. 2010; Camargo & Oliveira 2012), thus expanding the accessible resource base and producing a relatively continuous canopy surface (Emmons & Gentry 1983; Putz 1984).

Lianas also provide a variety of spatially and temporally predictable food sources that are consumed (or potentially consumed) by ants, including extrafloral nectaries (EFNs), insect exudates (i.e., hemipteran “trophicbionts”), floral nectar, fruits, seeds, and pollen (Bentley 1981; Baroni Urbani & de Andrade 1997; Blüthgen et al. 2000; Pizo & Oliveira 2000; Davidson et al. 2003; Rico-Gray & Oliveira 2007). Many lianas flower and fruit out of phase with trees in seasonal forests (e.g., in Panama: Opler et al. 1991), thereby reducing temporal gaps in the availability of these nutritional resources. More importantly, EFNs and trophobionts tend to be more abundant on lianas than on trees (Blüthgen et al. 2000; Blüthgen & Fiedler 2002), and these resources fuel the aggressive activities of *Azteca* and other behaviorally dominant arboreal ants (Davidson 1997; Yanoviak & Kaspari 2000; Rico-Gray & Oliveira 2007). Thus, carbohydrates derived from lianas may determine local ant community structure in the tropical forest canopy by direct bottom-up effects or via tritrophic interactions (Blüthgen et al. 2004; Rico-Gray & Oliveira 2007).

The relatively narrow, linear structure of lianas also appears to be an important resource for arboreal ants (Clay et al. 2010; Yanoviak et al. 2012). Unlike flying central-place foragers (e.g., bees), for which foraging imposes significant energetic costs, *time* is the major cost of foraging in cursorial organisms like ants (Fewell 1988). Time is related to foraging distance, and a
trade-off should exist between the benefits of rapid discovery or dominance of high quality (or distant) resources (Hölldobler & Wilson 1990; Davidson 1998; Adler et al. 2007), and the cost of time spent outside the nest. A worker’s risk of becoming lost, and its exposure to competitors, predators and pathogens, increases with time spent away from home. Thus, ants should select the most efficient route when foraging. Whereas ground-dwelling ants tend to choose pathways that maximize their two-dimensional velocity (Fewell 1988; Dussutour et al. 2006; Farji-Brener et al. 2007), similar patterns remain relatively unexplored in arboreal ants. The forest canopy offers a particularly interesting evolutionary scenario for such studies because access to patchy resources is constrained by the reticulate structure of the habitat.

Many arboreal ant species preferentially use lianas as foraging trails even in the absence of EFNs or trophobionts (Bentley 1981; Yanoviak et al. 2012), suggesting that structural characteristics of liana stems enhance ant foraging efficiency. Results of our field studies in Costa Rica support this hypothesis; upon discovering a high-quality food item on a tree trunk, ants altered the location of their foraging trails to incorporate nearby climbing plant stems and hemiepiphyte roots, and behaviorally dominant ants defended such pathways (Clay et al. 2010). We also explored the effects of fine-scale liana stem characteristics on ant foraging by placing artificially high quality resources (tuna baits) on stems classified quantitatively by size (diameter), and qualitatively by roughness and type (herbaceous vs. woody). Liana substrate properties, especially stem diameter and roughness, influenced the distribution of foraging ants in the forest based on body size. Specifically (and not surprisingly), the largest ants were uncommon on the smallest stems except when enticed by baits (Yanoviak et al. 2012).

Although comparative data are not yet available, lianas generally appear to have relatively smooth surfaces that offer less costly foraging routes for ants than do tree branches and trunks. Our pilot studies show that ant running speed is significantly reduced when the height of the obstacles (i.e., the rugosity of a plant surface) is approximately 33% of the worker body’s length (Silveri & Yanoviak, unpublished data). Similar patterns occur in cockroaches (Sponberg & Full 2007), and it is reasonable to expect the scaling of dynamic instability to be consistent among arthropods with a tripod gait. This relationship deserves further exploration specifically in light of the size-grain hypothesis, the surface properties of plant stems, and leg allometry in ants (Kaspari & Weiser 1999; Farji-Brener et al. 2004; Sarty et al. 2006).

**ANT ASSOCIATIONS WITH OTHER CLIMBING PLANTS**

Apart from lianas, various herbaceous climbing plants and hemiepiphytes also provide important resources for ants and other arthropods in tropical forests. Whereas lianas are a reliable and widespread source of horizontal connectivity within the forest canopy, ants commonly use the aerial roots of hemiepiphytes as vertical foraging pathways and canopy – understory corridors (Clay et al. 2010; Yanoviak, pers. obs.). Likewise, the slender ascending stems of climbing palms (rattans) in Asia provide connectivity and nest sites for ants and their associated Hemiptera (Moog et al. 2003; Edwards et al. 2010; Chan et al. 2012). One other example of ant use of tropical herbaceous climbers is particularly noteworthy for its specialization. The climbing insectivorous pitcher plant *Nepenthes bicalcarata* has a remarkable association with the ant *Camponotus schmitzi* in Borneo. As in other ant–plant mutualisms, the plant provides nectar and shelter for the ants while the ants provide protection for the plant against herbivory (Merbach et al. 2007). However, *C. schmitzi* workers also prevent trapped insect prey from escaping the pitchers, and forage on the victims by swimming in the plant’s capture fluid (Clarke & Kitching 1995). Although this superficially appears detrimental to the plant, closer examination showed that the ants subsequently return unconsumed insect fragments to the pitcher (Clarke & Kitching 1995; Bonhomme et al. 2011). As noted above, similar mutualistic associations between ants and climbing vegetation are unknown in the neotropics.

In summary, lianas and other climbing plants play important ecological and evolutionary roles for arthropods in tropical forests. In particular, cursorial organisms like ants depend on the structural contributions of lianas to facilitate their foraging activities and territoriality, and the relatively abundant green tissues of lianas are a key resource for herbivores. However, most information regarding associations between arthropods and lianas remains observational or anecdotal. Given that liana abundance is increasing in tropical forests (e.g., Schnitzer & Bongers 2011; Schnitzer, Chapter 30 in...
this volume), there is a growing need for manipulative studies designed to isolate the specific contributions of lianas to arthropod diversity in the canopy.

**EFFECTS OF LIANA EXTERMINATION ON ARBOREAL ANT COMMUNITIES**

If lianas provide important resources for ants and other arboreal animals, we expect changes in liana abundance to have important bottom-up effects on local species richness in the forest canopy. My students and I are testing this hypothesis by measuring the effects of a replicated, large-scale liana removal experiment on arboreal ant community structure in a Panamanian forest (described below). Our ongoing experiments focus on three predictions. First, given that lianas provide food and nest sites that are used by ants, we expect the local (i.e., within-tree) species richness of ants to decline following liana removal. Second, we predict that effects of liana removal on ant species richness will be counteracted by the addition of artificial nest sites and inter-tree connectivity. Finally, we expect the increased isolation of tree crowns following liana removal to cause local extinctions of behaviorally dominant ants, specifically *Azteca* spp.

Stefan Schnitzer and colleagues established a large-scale liana removal experiment in Panama in 2008. The project consists of 16 forest plots $80 \times 80$ m on the Gigante Peninsula of the Barro Colorado Natural Monument (09.123°N, 79.857°W). Within each plot, all trees, lianas and shrubs $>1$ cm dbh ($>25,000$ individuals) were identified, tagged and measured following standard plot census protocols for lianas (Gerwing et al. 2006; Schnitzer et al. 2008) and trees (Condit 1998). In April 2011, all lianas in 8 of the 16 plots were exterminated by cutting their stems in the understory. The effects of the manipulation were conspicuous in the canopy within a few weeks (Fig. 24.1), and resulted in increased light in the understory over a period of months (Fig. 24.2). Approximately 95% of liana biomass had fallen from the Gigante canopy by June 2012 (Yanoviak, pers. obs.). We collected arboreal ants from the trunk and crown of five or six trees in each plot before liana cutting, as well as 2, 8, and 14 months after liana cutting. We climbed each tree using the single-rope method (Perry 1978) and collected ants by hand and with tuna baits for up to 2 hours per tree in fair weather. Variables recorded included air temperature, relative humidity, tree size (dbh), tree species, total time spent in the tree, and a qualitative assessment of weather conditions.

We also quantified the abundance of *Azteca trigona/chartifex* nests (Fig. 24.3) by conducting systematic visual scans of the midstory and canopy (i.e., point counts) within each plot. *Azteca trigona/chartifex* are polydomous, and well-established colonies often have one or two very large nests and several smaller nests scattered within a 10–20 m radius (Fig. 24.3). Thus, to avoid artificial inflation of nest counts and to provide an accurate approximation of actual colony density, we counted multiple nests in a single tree and multiple nests located within a few meters of each other as a single nest.

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**Fig. 24.1** Dead lianas were conspicuous in the canopy of liana removal plots within weeks of cutting their stems in the understory. (Source: S.P. Yanoviak. Reproduced with permission.) See plate section for color representation of this figure.

**Fig. 24.2** Liana cutting increased light penetration to the understory in the months following the manipulation. (Source: S.P. Yanoviak. Reproduced with permission.) See plate section for color representation of this figure.
Effects of lianas on canopy arthropod community structure

To test the hypothesis that tree-to-tree connectivity provided by lianas affects arboreal ant community structure, we added used climbing ropes (i.e., artificial liana stems) to several focal trees in each plot. The ropes were loosely tied around the main branches of neighboring trees (Fig. 24.4), and were used by ants to move from tree to tree almost immediately. We similarly tested for possible nest-site limitation in the canopy by adding 10 artificial twig nests to the crowns of up to three trees per plot. These nests consisted of aluminum or brass tubing 10 cm in length and closed at one end. Tubes were taped together in pairs or triplets and secured with nylon ties to the undersides or other protected portions of branches (Fig. 24.5). Finally, in 2013 we installed potted lianas in the crowns of selected trees. Over the coming years, these potted lianas will be pruned to confine their growth to a single tree crown, thus enabling us to test the hypothesis that lianas influence ant diversity via resources beyond connectivity and nest sites.

**LIANA REMOVAL REDUCES LOCAL ANT SPECIES RICHNESS**

To date, we have collected ca. 100 ant species or morphospecies from the Gigante plots. The number of ant species per tree ranged from 4–20, which is consistent with other studies of resident ants in tropical trees (Tanaka et al. 2010; Klimes et al. 2012). The number of ant species in our collections will likely increase as we continue with species identification and confirmation.

Average ant species richness in focal trees of liana removal plots declined by 22% relative to controls approximately one year after the lianas were cut. Two taxa, *Pachycondyla* spp. and *Cephalotes basalis*, showed the most consistent reduction in tree occupancy following liana removal. We attribute the loss of...
Fig. 24.5 Approximately 500 artificial twig nests were constructed from brass and aluminum hobby tubing closed at one end and secured to tree branches in the canopy. Each tube is 10 cm long and tube diameters ranged 2–5 mm. (Source: S.P. Yanoviak. Reproduced with permission.)

Pachycondyla mainly to the reduction of physical connectivity between trees. Pachycondyla spp. are roaming, often specialized predators (e.g., Davidson et al. 2003), and their conspicuous use of artificial connectivity in liana removal plots (see below) suggests that their local distributions are dependent on access to broad foraging areas provided by inter-tree connections. Local declines in Cephalotes basalis were most likely due to loss of nest sites. Although they commonly inhabit cavities in living and dead tree branches, the C. basalis colonies we found on Gigante were almost always in large liana stems, and thus the natural history of this species and its association with lianas deserve further study. Despite the overall trend for reduced ant diversity following liana cutting, species richness increased in some trees in the liana removal plots. Almost all such cases were the result of Camponotus spp. (carpenter ant) colonization of dead lianas that had not yet fallen from the canopy. These effects are expected to disappear as the few remaining lianas decompose.

An exploratory Principal Components Analysis (PCA) showed a positive relationship between tree size, time spent in a tree, and ant species richness, which was driven by the tendency to spend less time in trees having fewer species, rather than by sampling error. The PCA also showed no positive associations between tree species identity or local environmental conditions on ant species richness. These results concur with other studies suggesting that arboreal arthropod communities are more strongly influenced by differences in structural properties (e.g., size) among trees rather than tree species identity (Stork 1987; Tanaka et al. 2010; Klimes et al. 2012).

Liana cutting had conspicuous short-term effects on ant behavior and the abundance of other taxa. We found significantly fewer ants foraging in trees two months after liana cutting; ant recruitment to baits was slower, and more time was required to thoroughly census each tree in the treatment plots. Also, the abundance of beetles (especially wood borers and fungus feeders), woodpeckers, and web-building spiders was conspicuously higher in liana removal plots shortly after liana cutting. Presumably, the pulse of dead wood and decaying foliage attracted the beetles, which subsequently attracted the woodpeckers. The conspicuous increase in spider density was likely a result of increased light availability (e.g., Lubin 1978), though data are needed to verify this observation and the other patterns described above.

The addition of artificial connectivity (old ropes) had positive effects on ant species richness in trees of both control and liana removal plots. Addition of connectivity to trees in control plots increased ant species richness by ca. 25% from June 2011 to June 2012, whereas trees in liana removal plots without added ropes lost ca. 30% of their ant species over the same time interval. Although connectivity did not completely compensate for the effects of liana removal, these trends suggest that the presence of connectivity is an important determinant of ant species richness in tropical trees. Species of all common arboreal ant genera readily used the added connectivity in both control and liana cut plots. Azteca spp. and Pachycondyla spp. consistently used the ropes, and Azteca trigona/chartifex constructed carton around the rope–tree connection point in some cases. We also commonly observed multiple genera (e.g., Azteca, Camponotus, Cephalotes, Pachycondyla, and Pseudomyrmex) simultaneously using a single rope. Rather than partition the rope into separate foraging pathways, unrelated ants simply
avoided contact with each other and continued their forward progress.

In contrast to the connectivity addition experiment, the addition of artificial twig nests was unsuccessful. Approximately 10% of the ca. 500 artificial twig nests we installed in the canopy had fallen or were missing after one year. Less than 1% of the remaining artificial nests were colonized by ants, and ca. 10% were occupied by other taxa, especially spiders. Low occupancy of these artificial nests may be a consequence of using metal tubes, which we chose for their durability. However, other studies using wood or bamboo artificial nests also observed relatively low (<30%) occupancy by ants (Philpott & Foster 2005; Philpott 2010; Sagata et al. 2010). By contrast, naturally occurring cavities in living and dead twigs tend to have high ant occupancy, suggesting that ants are nest-limited, but also very selective with respect to nest characteristics.

Liana removal had strong effects on Azteca nest densities. The average number of Azteca nests increased at approximately twice the rate in liana removal plots as in control plots over the two years after cutting. Because Azteca trigona/chartifex are polydomous, we could not clearly distinguish between expansion of existing colonies and the founding of new colonies based on our field surveys. Regardless, it is clear that Azteca abundance increased on liana removal plots. We attribute this increase to three factors, all of which are purely speculative at this point. First, greater light availability and associated warmer temperatures may have stimulated colony activity and expansion. Second, the pulse of relatively labile dead wood in liana cut plots, which is used to construct carton nests, could have promoted the growth of existing nests. Third, the absence of lianas may have prevented anteaters (Tamandua mexicana) from accessing Azteca nests. This latter explanation (perhaps in combination with other mechanisms) seems most likely; our preliminary observations of foraging anteaters showed that they use lianas almost exclusively when accessing the canopy. Given that Azteca are among the most aggressive arboreal ants in neotropical forests, their increased local abundance and the increased isolation of their resident trees may result in competitive exclusion of subordinate species over the short term (Catling 1997; Vandermeer et al. 2010). We further expect that this process will occur more slowly in trees with added artificial connectivity, as explained above.

Although liana removals resulted in increased Azteca density over the two years after cutting, we suspect that the role of Azteca will become diminished in liana removal plots over the long term. This prediction is based on two assumptions that remain to be tested. First, liana-based EFNs and trophobionts (honeydew-producing herbivores) are important sources of the carbohydrates that fuel high-tempo, aggressive taxa like Azteca (Davidson 1997; Blüthgen & Fiedler 2002; Blüthgen et al. 2004). Assuming Azteca, their trophobionts, and lianas are involved in specialized tritrophic interactions, liana removal should cause localized Azteca extinctions, facilitating the coexistence of subordinate ant species via competitive release (though such effects are difficult to demonstrate, even in much simpler systems; e.g., Kareiva 1982; Riechert & Cady 1983). Second, we assume that physical connectivity in the canopy is essential for the maintenance of large Azteca colonies. If so, the physical isolation of tree crowns should dramatically reduce Azteca foraging efficiency, and eliminate their access to colony subunits and distant resources. The conspicuous use of artificial connectivity by Azteca foragers in liana removal plots (see above) suggests that the absence of such pathways will make large colonies unsustainable, though this remains to be determined.

Collectively, the preliminary results of this large-scale experiment suggest that lianas are important determinants of local species richness in arboreal ant communities. Although strong effects of liana removals and added connectivity appeared just one year after the manipulation, uncovering the mechanisms behind these effects will require many more years of data collection. Future censuses will enable us to determine if the observed changes in species richness are driven specifically by the absence of lianas, or by more generalized effects of large-scale disturbance. Liana removal clearly resulted in greater light penetration due to the significant reduction in canopy cover (Figs. 24.1, 24.2). This change resembles natural phenomena that also cause significant canopy defoliation while leaving standing trees, such as hurricanes (e.g., Tanner et al. 1991), seasonal drought stress (Dietrich et al. 1982; Boinski & Fowler 1989), large lightning strikes (Magnusson et al. 1996; Richards 1996; Yanoviak 2013), and pathogen outbreaks (e.g., Wong et al. 1990). Such disturbances should promote population growth or persistence of species that are tolerant of high light conditions and associated thermal and desiccation stress, as appears to be occurring for Azteca in the liana removal plots. Regardless, if the observed
changes in ant communities are an artifact of collateral abiotic effects of liana removal, such effects will dissipate as tree crowns grow into the spaces left by liana foliage, which tends to occur relatively rapidly (Kira & Ogawa 1971). Ultimately, the great advantage of this large-scale experiment is that the specific contributions of lianas to arboreal ant community structure will become increasingly clear over time.

CONCLUSION AND FUTURE DIRECTIONS

Lianas are conspicuous components of tropical forests, yet we are just beginning to understand their effects on the ecology of arthropods and other consumers. Resolving this information deficit is important given that increasing liana abundance may be a key driver of changes in tropical forest structure over the next century. One fundamental question provides a solid basis for future work on this problem: Are lianas functionally redundant with trees, shrubs and epiphytes, or does the liana growth form provide a unique ecological template within tropical forests? To date, the only focused attempts at answering this question from the perspective of arthropods come from painstaking inventories of herbivorous insects and our experimental studies of arboreal ants. In particular, Ødegaard’s (2000b) beetle surveys suggest that the large ratio of foliage to total plant biomass and the relatively high production of new growth make lianas important bottom-up contributors to arthropod diversity in the canopy, and our ongoing research in Panama indicates that a unique structural contribution of lianas—physical connectivity among tree crowns—is an important determinant of local arboreal ant diversity.

These studies are just the beginning of exploration into liana–arthropod interactions, and answers to even relatively basic questions would greatly enhance our understanding of the ecological contributions of lianas to arthropod diversity. For example, how do arthropod assemblages associated with lianas change seasonally; i.e., does the composition of herbivores and other associates vary seasonally or over the lifetime of a liana? Is liana species richness a good predictor of arthropod species richness at regional scales? If so, what liana traits determine the composition and diversity of their arthropod associates? Finally, is the contribution of lianas to canopy arthropod diversity additive or synergistic with other forest components? The study of liana-arthropod relationships may provide a fruitful avenue for exploring specific relationships between arthropods and their specific plant hosts, as well as more general research questions on plant-animal and tritrophic interactions.

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REFERENCES


Fig. 24.1 Dead lianas were conspicuous in the canopy of liana removal plots within weeks of cutting their stems in the understory. (Source: S.P. Yanoviak. Reproduced with permission.)

Fig. 24.2 Liana cutting increased light penetration to the understory in the months following the manipulation. (Source: S.P. Yanoviak. Reproduced with permission.)