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Benjamin J. Adams
University of Louisville

Evan M. Gora
University of Louisville

Michiel van Breugel
Smithsonian Tropical Research Institute

Sergio Estrada-Villegas
Marquette University

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

See next page for additional authors

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Authors

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Do Lianas Shape Ant Communities in An Early Successional Tropical Forest?

Benjamin J. Adams

Department of Biology, University of Louisville, Louisville, KY
Urban Nature Research Center, Natural History Museum of Los Angeles County, Los Angeles, CA

Evan M. Gora

Department of Biology, University of Louisville, Louisville, KY

Michiel van Breugel

Yale - NUS College, Singapore, Singapore

Department of Biological Sciences, National University of Singapore, Singapore, Singapore
Smithsonian Tropical Research Institute, Balboa, Panama

Sergio Estrada - Villegas

Smithsonian Tropical Research Institute, Balboa, Panama
Department of Biological Sciences, Marquette University, Milwaukee, WI

Stefan A. Schnitzer

Smithsonian Tropical Research Institute, Balboa, Panama

Department of Biological Sciences, Marquette University, Milwaukee, WI

Jefferson S. Hall

ForestGEO, Smithsonian Tropical Research Institute, Balboa, Panama

Stephen P. Yanoviak

Department of Biology, University of Louisville, Louisville, KY

Smithsonian Tropical Research Institute, Balboa, Panama

Abstract

Almost half of lowland tropical forests are at various stages of regeneration following deforestation or fragmentation. Changes in tree communities along successional gradients have predictable bottom-up effects on consumers. Liana (woody vine) assemblages also change with succession, but their effects on animal succession remain unexplored. Here we used a large-scale liana removal experiment across a forest successional chronosequence (7–31 years) to determine the importance of lianas to ant community structure. We conducted 1,088 surveys of ants foraging on and living in trees using tree trunk baiting and hand-collecting techniques at 34 paired forest plots, half of which had all lianas removed. Ant species composition, β -diversity, and species richness were not affected by liana removal; however, ant species co-occurrence (the coexistence of two or more species in a single tree) was more frequent in control plots, where lianas were present, versus removal plots. Forest stand age had a larger effect on ant community structure than the presence of lianas. Mean ant species richness in a forest plot increased by ca. 10% with increasing forest age across the 31-year chronosequence. Ant surveys from forest >20 years old included more canopy specialists and fewer ground-nesting ant species versus those from forests <20 years old. Consequently, lianas had a minimal effect on arboreal ant communities in this early successional forest, where rapidly changing tree community structure was more important to ant species richness and composition.

1 INTRODUCTION

Tropical forests contain more than half of all terrestrial biodiversity yet occupy a relatively small area of Earth (Raven, **1988**). Deforestation and fragmentation remain major threats to tropical biodiversity, and ca. 30% of neotropical forests are in early stages of secondary succession (Chazdon et al., **2016**). Although plant community succession is well characterized, and conspicuously shapes animal communities (Bihn, Verhaagh, Brändle, & Brandl, **2008**; Dunn, **2004**; Finegan, **1996**; Pielou, **1966**; Smith, **1928**; Sousa, **1979**), the mechanisms by which specific habitat characteristics change animal communities during succession are poorly understood.

Tropical forest succession is characterized by changes in the relative abundance, size, and species composition of trees and vines (Huston & Smith, **1987**; Letcher & Chazdon, **2009**; Uhl, Buschbacher, & Serrao, **1988**). Succession alters the physical structure of a forest via increased tree biomass, height, and crown complexity (Aide, Zimmerman, Herrera, Rosario, & Serrano, **1995**; Guariguata & Ostertag, **2001**). At the same time, tree and liana (woody vine) stem density typically decreases during later stages of forest succession (Chazdon et al., **2007**). These changes affect habitat structure and species interactions (Purschke et al., **2013**) with predictable effects on animal community structure (Bihn et al., **2008**; Dunn, **2004**; Smith, **1928**). Whereas tree size and species composition have demonstrated bottom-up effects on animal succession (Campos, Vasconcelos, Ribeiro, Neves, & Soares, **2006**; Klimes et al., **2012**; Ribas, Schoereder, Pic, & Soares, **2003**), the role of lianas in this context is unclear.

Lianas represent a substantial proportion of plant stem density, plant diversity, and physical complexity in lowland tropical forests (Gianoli, **2015**; Ingwell, Wright, Becklund, Hubbell, & Schnitzer, **2010**; Lai, Hall, Turner, &

van Breugel, 2017; Putz, 1984; Schnitzer & Bongers, 2002; Yanoviak & Schnitzer, 2013). Lianas provide key resources to arboreal animals, including food and nest sites (Blüthgen et al., 2000; Tanaka & Itioka, 2011). Thus, changes in liana abundance and species composition during succession (Barry, Schnitzer, van Breugel, & Hall, 2015; Lai et al., 2017; Letcher & Chazdon, 2009) should have substantial bottom-up effects on animal community structure via changes in liana-based resources (Estrada-Villegas & Schnitzer, 2018). Lianas also influence arboreal animal distributions by connecting neighboring treecrowns (Adams, Schnitzer, & Yanoviak, 2017, 2019; Chiarello et al., 2004; Yanoviak, 2015), which are otherwise commonly isolated in space due to “crown shyness” (the tendency for a physical gap to exist between neighboring trees within a forest canopy; Ng, 1977; Putz, Parker, & Archibald, 1984). However, the contribution of lianas to inter-crown connectivity presumably is minimal during early succession due to the inherently small stature and dense packing of treecrowns in young forest (Aide et al., 1995; Montgomery & Chazdon, 2001). The importance of lianas for arboreal animals likely increases in later successional stages as trees become increasingly isolated due to crown shyness (Putz et al., 1984).

Ants represent a significant portion of total animal biomass and insect abundance in forest canopies (Blüthgen & Stork, 2007; Davidson, Cook, Snelling, & Chua, 2003; Floren, Wetzell, & Staab, 2014), and are a good model taxon for studying arboreal communities across forest successional stages (Floren, Freking, Biehl, & Linsenmair, 2001; Klimes et al., 2012; Silva, Feitosa, & Eberhardt, 2007). Arboreal ant species richness and functional diversity typically increase during forest succession (Bihn et al., 2008; Dunn, 2004; Marques, Espírito-Santo, Neves, & Schoereder, 2017; Silva et al., 2007), in part due to overall increases in tree size and diversity, and nest site availability (Campos et al., 2006; Klimes et al., 2012; Ribas et al., 2003). As individual trees age and grow taller, the resident ant community also changes to include fewer ground-nesting species (Dejean, Djiéto-Lordon, Céréghino, & Leponce, 2008; Tschinkel & Hess, 1999). In older forests, lianas physically connect isolated treecrowns and support higher local (i.e., per-tree) ant species richness, specifically benefiting ant species with wide-ranging foraging strategies (e.g., *Neoponera* spp., *Paraponera clavata*; Davidson, 1997; Yanoviak & Schnitzer, 2013; Adams, Schnitzer, et al., 2017, 2019). However, the ecological effects of lianas on ants are unknown for early stages of forest succession.

We used a large-scale liana removal experiment in 17 forest sites to determine the effects of lianas on arboreal ant community structure along a 31-year chronosequence in a neotropical forest. Based on observations and liana removal experiments in older forests (Adams et al., 2017; Adams, Schnitzer, et al., 2019), we hypothesized that lianas positively influence ant community structure (e.g., species composition, species richness, β -diversity, and species co-occurrence) in early secondary tropical forests. Accordingly, we evaluated four associated predictions. First, trees with lianas will have higher ant species richness compared to trees without lianas. Second, ant species composition in trees with lianas will include more wide-ranging foragers. Third, trees with lianas will have lower ant β -diversity compared to trees without lianas. Finally, patterns of ant co-occurrence will differ between trees with lianas versus trees without lianas, presumably due to increased interactions resulting from increased connectivity. Due to the low height of the canopy and lack of crown shyness in young forests (Aide et al., 1995), we expect lianas to have the greatest effect on ant communities in later stages of forest succession.

2 METHODS

2.1 Study site

Fieldwork was conducted in central Panama at the Agua Salud Project (hereafter, Agua Salud; 09.210°N, 79.745°W) administered by the Smithsonian Tropical Research Institute (Stallard, Ogden, Elsenbeer, & Hall, 2010). Agua Salud is a seasonally moist secondary forest that receives an average of 2,700 mm of rain each year, mostly from May to December, located on hilly terrain with steep slopes that were previously degraded

agricultural lands (van Breugel et al., **2013**; Ogden, Crouch, Stallard, & Hall, **2013**). Croat (**1978**) and Leigh, Rand, and Windsor (**1996**) provide more information about the region. The liana removal experiment (described below) is part of the Agua Salud secondary forest dynamics network. Details about this network are provided in van Breugel et al. (**2013**), Van Breugel et al. (**2019**) and Craven, Hall, Berlyn, Ashton, and van Breugel (**2015, 2018**).

Agua Salud includes 52 forest sites along a 31-year chronosequence of forest succession following agricultural field abandonment (van Breugel et al., **2013**). Thirty sites contain two non-contiguous 20 × 50 m plots, each marked by a 5 × 5 m grid, located on the upper portion of a slope. One plot in each site had all lianas (woody vines) removed in 2013 and was maintained liana-free throughout the project following the methods used in a nearby older secondary forest (van der Heijden, Powers, & Schnitzer, **2015**). Total aboveground biomass, tree basal area, and individual stem counts were measured prior to liana removal and annually after the removal treatment in each subplot (van Breugel et al., **2013**). We selected 34 paired plots for this study (i.e., 17 forest sites, each with one liana removal and one control plot) based on accessibility.

2.2 Ant surveys

We censused the arboreal ant communities using baiting and hand collecting during the wet seasons (May–September) in each plot prior to liana removal in 2012 and 2 years after liana removal in 2015. Collections were made on the largest tree (determined as diameter at breast height; DBH) nearest to each of 16 predetermined locations within each plot. The first four locations were at the four corners of the plot, and the remaining 12 locations equidistantly spaced among the internal points of the 5 × 5 m grid (**Figure S1**). The sampled trees averaged *ca.* 10 cm DBH; only 6% were ≥20 cm DBH and 23% of trees were ≤5 cm DBH during the time span of this study. Due to the low canopy height (<5 m), and small tree sizes in most plots (van Breugel et al., **2013**), it was not feasible to sample ants via tree climbing. Instead, we standardized the survey method by baiting and hand collecting from the ground. We placed baits (a mixture of canned tuna in water and honey; roughly 140 g tuna to 30 ml honey) on each tree at a height of *ca.* 2 m. We recorded the presence of different ant species on a tree by collecting representative ant workers both at the baits and elsewhere on the tree (all accessible locations on the tree or associated lianas, including any branches, all liana stems, and all sides of the trunk) *ca.* 30 min. after bait placement. We stored collected ants in 95% ethanol and identified all specimens to species or morphospecies using published keys (e.g., Longino, **2007**; Ward, **1989, 1999**; Ward, Brady, Fisher, & Schultz, **2010**). Ant species nesting preferences (ground vs. canopy, if known) were determined from natural history descriptions provided in the taxonomic literature and online resources (AntWeb, **2019**). Reference specimens were confirmed by taxonomists, and vouchers were deposited at the University of Louisville; the United States National Museum, Washington DC; the Smithsonian Tropical Research Institute, Panama; and the Fairchild Museum at the University of Panama.

2.3 Analysis

We used the plot as our experimental unit for analyses because liana removal treatments were applied at the plot level, and because the number of ant species on individual trees within a plot was highly variable (mean ± SE: 1.3 ± 1.1 species, range: 0–6). We used species accumulation curves to estimate the fraction of the total arboreal ant species richness of Agua Salud that was sampled in this study (EstimateS version 9.1.0; Colwell, **2009**). We subsequently used a mixed-effect linear model to test for differences in species richness (*lme4* package; Bates, Mächler, Bolker, & Walker, **2015**; R Core Team, **2018**; R version 3.5.0), and a mixed-effect PERMANOVA and PERMDISP with 9,999 iterations (Anderson, Gorley, & Clarke, **2008**; Anderson et al., **2011**; PRIMER version 6.1.18 with PERMANOVA+ package 1.0.8) to test for differences in species composition and β-diversity, respectively.

All models originally included collection year, stand age, and treatment (liana removal vs. control) as fixed effects, along with all interaction terms, and site as a random factor. We performed nested model reduction using differences in AIC values and likelihood ratio tests. None of the interaction terms was significant, and the model with the lowest AIC value did not include the random site effects. We used indicator species analysis to identify ant species that were strongly associated with significant terms from the PERMANOVA (de Cáceres & Legendre, 2009; Dufrene & Legendre, 1997). Following results of the indicator species analyses, we ran two post hoc ANOVAs exploring how the proportion of strictly arboreal ants and strictly plus facultatively arboreal ants (species reported to nest both on the ground and in trees) in each plot changed both across collection years and the continuous chronosequence. Finally, we created NMS ordinations (200 runs, 500 iterations, and random starting configuration) to visualize differences in species composition among ant communities associated with significant terms from the PERMANOVA.

We log-transformed species richness data, confirmed normality using the Shapiro–Wilk test on the residuals, and examined residuals to confirm model fit. We calculated similarity matrices for species composition analyses using the Jaccard index to accommodate the presence/absence data structure (i.e., each ant species was treated as either present or absent because abundance values for social insects require direct nest counts). The resulting distance matrix was used to perform PERMANOVA, PERMDISP, and the NMS ordination. PERMANOVA and PERMDISP require categorical variables; therefore, we transformed stand age into a categorical variable representing three successional stages (<10 years old, 10–20 years old, and >20 years old) based on differences in biomass ($F_{2,14} = 8.16, p = .004$) and basal area ($F_{2,14} = 10.38, p = .002$) among age groups.

2.4 Species co-occurrence

We calculated C-scores to determine if arboreal ant communities followed non-random patterns of species co-occurrence and if the removal of lianas changed these patterns (Blüthgen & Stork, 2007; Majer, 1976; Sanders, Crutsinger, Dunn, Majer, & Delabie, 2007). A C-score index compares patterns of co-occurrence in observed communities against a null model with a random distribution (Gotelli, 2000; Gotelli & Ulrich, 2012). We used EcoSimR 1.0 (Gotelli & Ellison, 2013) to examine co-occurrence frequencies in individual trees, and for the entire plot, in liana removal and control plots from the 2012 and 2015 surveys. We generated 9,999 randomized matrices using a fixed–fixed algorithm for ant species and for individual trees or plots surveyed. We chose a fixed–fixed algorithm because ant species differed in their total collection frequencies and different individual trees or plots potentially provide different resources and conditions for ants (Gotelli, 2000; Tschinkel & Hess, 1999).

3 RESULTS

The 1,088 tree surveys yielded a total of 91 ant species (Table S1), which represented ca. 76% of the species predicted to occur at this site using hand and bait collection methods (Figure S2). We found an average ($\pm SE$) of 11.1 ± 0.3 ant species per plot.

Liana removal resulted in only minor changes in ant community structure during early stages of forest succession. Ant species richness ($F_{1,64} = 0.03, p = .87$; Figure 1), composition (*Pseudo*- $F_{1,29} = 1.03, p = .41$), and β -diversity ($F_{1,33} = 0.11, p = .75$) were similar between the liana removal and control treatments, with no significant interactions among treatment, year, or stand age ($F < 0.92, p > .34$). However, there were differences in species co-occurrence patterns among individual trees between removal and control treatments in the 2015 survey. Specifically, ant species distributions did not differ from random in trees of the liana removal treatment (observed \leq simulated $p = .87$; observed \geq simulated $p = .13$), but showed a high frequency of co-occurrence in the control trees where lianas were present (observed \leq simulated $p < .0007$). By contrast, ant species co-occurrence at the individual tree level in the 2012 pre-treatment survey did not differ from random in either control or liana removal treatments (observed \leq simulated $p > .54$; observed \geq simulated $p > .10$). At the plot

level, ant species co-occurrence did not differ from random in control or removal treatments, nor during either collection year (observed \leq simulated $p > .41$; observed \geq simulated $p > .07$ for each test).

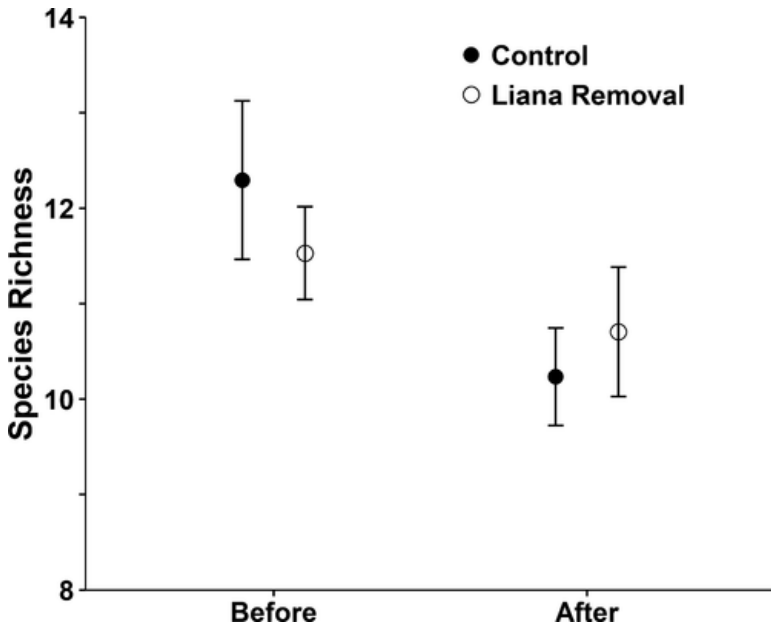


Figure 1 Ant species richness (mean \pm SE) in liana removal and control subplots in the 2012 (before treatment) and 2015 (after treatment) collections. Ant species richness did not differ between treatments within a year

Stand age influenced ant community parameters regardless of collection year or the presence of lianas. Ant species richness increased *ca.* 10% from the youngest to oldest forest stands (Figure 2; $F_{1,64} = 3.84$, $p = .05$, $R^2 = 0.04$), and ant species composition in the oldest plots (>20 years old) differed from plots that were <10 and 10–20 years old (Figure 3; *Pseudo-* $F_{2,56} = 1.49$, $p = .012$; $t > 1.26$, $P < .025$). *Neoponera carinulata*, an arboreal specialist of mature forest canopies (Mackay & Mackay, 2010), was common in the oldest age category of forest stands. By contrast, ant assemblages associated with earlier stand age categories included fewer strictly arboreal species and a larger fraction of ants that are commonly associated with early secondary forests (e.g., *Solenopsis picea*, Table 1).

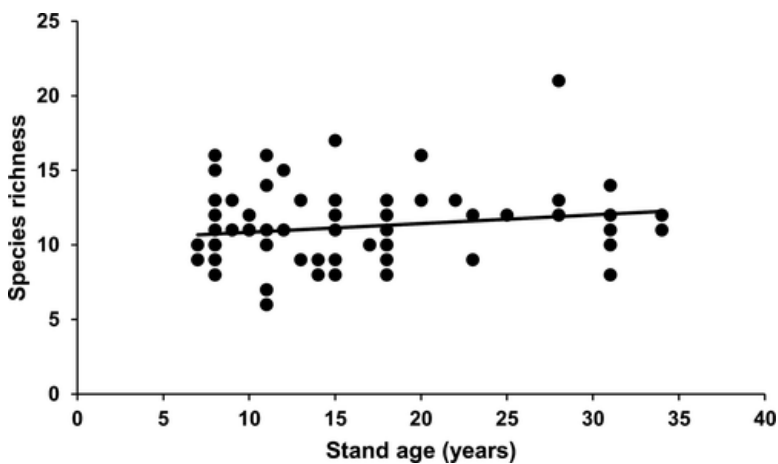


Figure 2 Ant species richness per plot versus plot age at time of collection (i.e., collections from the same plot will have different stand ages in 2012 and 2015). Collections from both years are pooled as there was no significant year*plot age interaction. Ant species richness increases with stand age as described by the equation richness = 0.058*Age + 10.27 ($F = 3.88$, $p = .05$, $R^2 = .04$)

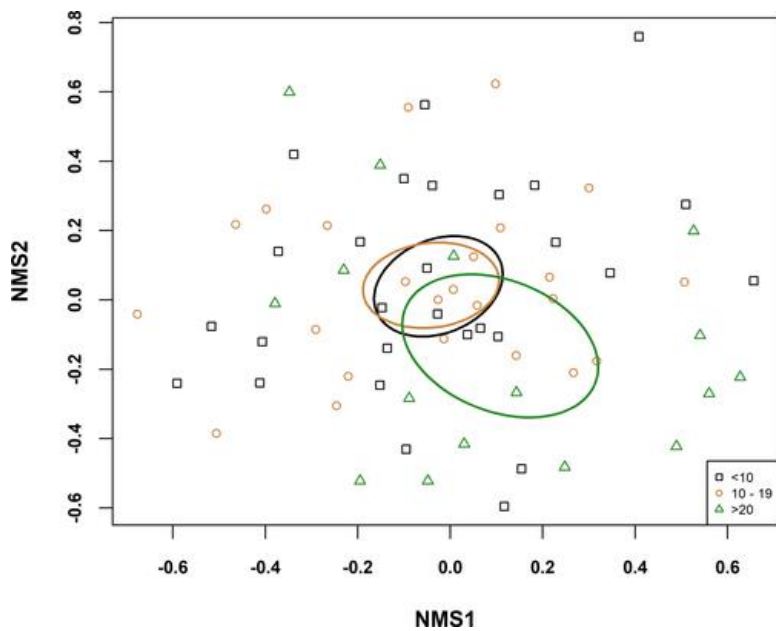


Figure 3 NMS ordination of plot-level ant species composition across the three forest stand age categories. The ellipses represent the 95% CI for location of the centroid in ordination space. Stress = 0.16

Table 1. Indicator species of ants in the three forest age categories (*Age range*), with their preferred nesting location (*Nest*), indicator values (*IndVal*), and adjusted *p*-values (*p*)

Age range	Ant species	Nest	IndVal	<i>p</i>
<10	<i>Procryptocerus belti</i>	Arboreal	0.423	.0243
10–19	<i>Solenopsis picea</i>	Both	0.435	.0434
≥20	<i>Crematogaster brasiliensis</i>	Arboreal	0.614	.0036
	<i>Neoponera carinulata</i>	Arboreal	0.495	.0172
	<i>Pheidole flavens</i>	Ground	0.397	.0379

Ant species composition also differed between the two collection years ($Pseudo-F_{1,56} = 3.18$, $p = .0001$, Figure 4). Several understory ant species were common in the 2012 collections (e.g., *Ectatomma* spp., *Pseudomyrmex boopis*), whereas arboreal species were more common in the 2015 collection (e.g., *Pseudomyrmex elongatus*; Table 2). The percentage (i.e., the fraction of the total collection for each plot) of strictly arboreal-nesting ants increased from 51% to 64% ($F_{1,59} = 16.05$, $p = .0002$) and strictly plus facultatively arboreal ants increased from 80% to 86% ($F_{1,56} = 8.42$, $p = .005$) between 2012 and 2015. By contrast, ground-nesting ants decreased from 48% to 35% over this time frame (Figure S3). Along with these differences in composition, overall ant species richness was ca. 10% higher in 2012 than in 2015 ($F_{1,63} = 5.54$, $p = .022$). The time between surveys represents a 33% increase in stand age in the youngest plots (7 years since abandonment in 2012 and 10 years in 2015) and a ca. 10% change in the oldest plots.

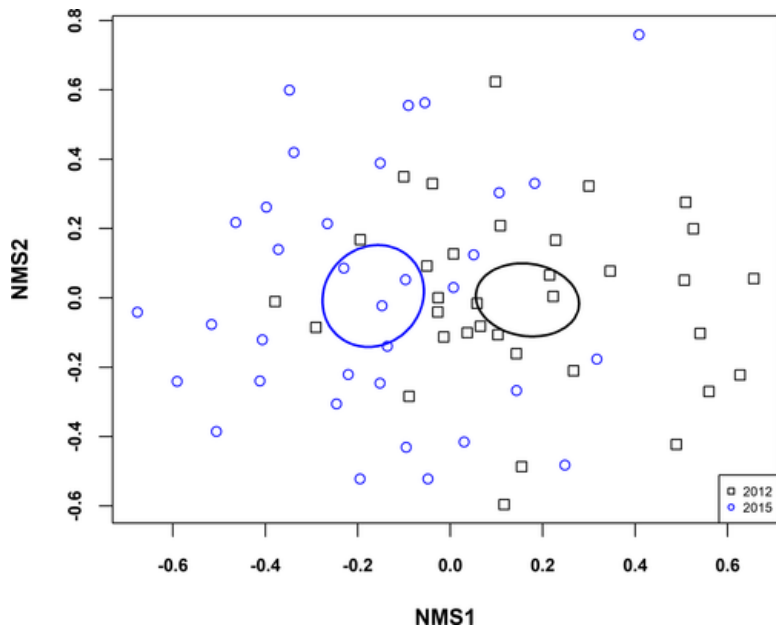


Figure 4 NMS ordination of plot-level ant species composition split between the two collection years. The ellipses represent the 95% CI for location of the centroid in ordination space. Stress = 0.18

Table 2. Indicator species of ants in each of the two collection years with their preferred nesting location (*Nest*), indicator values (*IndVal*), and adjusted *p*-values (*p*)

Year	Ant species	Nest	IndVal	<i>p</i>
2012	<i>Crematogaster carinata</i>	Arboreal	0.818	.0001
	<i>Ectatomma tuberculatum</i>	Ground	0.764	.0049
	<i>Ectatomma ruidum</i>	Ground	0.634	.0250
	<i>Pseudomyrmex boopis</i>	Both	0.628	.0002
	<i>Crematogaster brasiliensis</i>	Arboreal	0.614	.0051
	<i>Camponotus canescens</i>	Arboreal	0.485	.0045
	<i>Nylanderia guatemalensis</i>	Both	0.420	.0250
2015	<i>Camponotus brevis</i>	Arboreal	0.712	.0065
	<i>Crematogaster curvispinosa</i>	Arboreal	0.526	.0486
	<i>Solenopsis picea</i>	Both	0.425	.0274
	<i>Pseudomyrmex elongatus</i>	Arboreal	0.420	.0250

4 DISCUSSION

Plant communities set the stage for animal community assembly in most terrestrial ecosystems. Within forest habitats, changes in tree communities over time affect animal community structure, especially for arboreal taxa (Dunn, **2004**; Klimes et al., **2012**). Liana assemblages also change over the course of forest succession (Barry et al., **2015**; Letcher & Chazdon, **2009**) and provide valuable resources for arboreal animals (Yanoviak & Schnitzer, **2013**). However, here we show that lianas have a minimal effect on the structure of arboreal ant communities in early successional forests. Contrary to our predictions, liana removal did not reduce ant species richness, increase β -diversity, or consistently alter ant species composition in trees. In other studies where arboreal ant species richness was higher in the presence of lianas (Adams, Schnitzer, et al., **2019**), the forest was older, the canopy was higher, and individual trees were larger (Mascaro et al., **2011**) than in Agua Salud (van Breugel et al., **2013**). The results of this study suggest that a minimum threshold of forest age, canopy height, or

tree size is necessary before lianas affect arboreal ant community structure. The results also suggest that this threshold is not met in forest stands <30 years removed from intense agricultural use in central Panama.

Control plots in 2015 exhibited statistically significant ant species associations (i.e., ant co-occurrence patterns that differed from random). Increased connectivity among treecrowns provided by lianas could facilitate more frequent co-occurrence of ant species in a tree; however, previous work indicated that lianas had no effect on species co-occurrence in older forests (Adams et al., **2017**). Many potentially important ecological variables change as a forest develops, and the specific mechanisms underlying these ant species associations remain unknown. All stands used in this study also increased in age by >10% between sampling years, and plant composition is in a state of transition at this site (Craven et al., **2018**). Thus, understanding the specific mechanisms driving these differences in ant co-occurrence will require further study of interspecific interactions (e.g., competition, parasitism, and mutualisms) among ants, ant associations with certain tree and liana species, and ant responses to the distribution and composition of trophobionts (Davidson et al., **2003**; Fornoff, Klein, Blüthgen, & Staab, **2019**).

Lianas provide nest sites and reliable food resources for ants (Blüthgen et al., **2000**; Philpott, **2010**; Tanaka & Itioka, **2011**), and these resources should be important for ants regardless of forest age. Lianas also provide physical connections among treecrowns that are consistently used as foraging corridors by arboreal ants (Adams, Schnitzer, et al., **2019**; Yanoviak, **2015**). However, the functional role of connectivity should be relatively more important in older forests, where ant communities include more canopy specialists (Dejean et al., **2008**; Tschinkel & Hess, **1999**), and treecrowns typically lack physical contact with each other (Ng, **1977**; Putz et al., **1984**). The absence of a clear effect of liana removal on ant species richness and composition in this study suggests that nest sites and food resources provided by lianas were not limiting ant distributions in this forest. Additionally, connectivity among treecrowns was also not important to the ant communities likely because of the high frequency of ground-nesting ants, especially in the 2012 survey. Research on liana-based resources in a nearby older forest (>60 years old) found that connectivity was particularly important to the maintenance of arboreal ant diversity (Adams, Schnitzer, et al., **2019**). The increase in arboreal ant species in the 2015 survey suggests that lianas likely will become more important to the arboreal ant community as this forest continues to mature.

Differences in the ant community between sampling years can be attributed to differences in forest age. During the project time period, the youngest forest stands increased in age by >30%. Overall, the forest has experienced rapid, landscape-scale changes in tree species composition, species density, and functional diversity, as well as increases in overall stand basal area per plot (Craven et al., **2018**). Changes in tropical forest structure during succession affect ant communities (Floren et al., **2001**; Klimes et al., **2012**; Ribas et al., **2003**), typically with a shift in species composition toward more arboreal specialists (Dejean et al., **2008**). We similarly detected a change in ant species composition from ground-nesting to more arboreal ant species between the two sampling years. The loss of ground-nesting ants also likely caused the decrease in ant species richness observed in 2015 collections.

Finally, it is likely that our collection technique missed some arboreal ant species nesting in taller trees and disproportionately sampled ground-nesting ants, especially in older plots. Missing some canopy specialists in the older plots could explain the greater effect of collection year versus stand age on ant species composition, although it did not ultimately affect the results (both of these factors contributed to differences in the ant community). Regardless, given the short stature of most plots (average canopy height <5 m), we are confident that baiting trunks and low branches at heights of up to 2.5 m effectively attracted all of the common resident species in the focal trees.

In summary, arboreal ant communities appear to exhibit directional shifts in species composition and species richness during early forest succession, and the effects of lianas on ant community parameters are minimal during the earliest stages of forest regeneration. Given the importance of lianas in late-secondary and mature forests (Adams et al., 2017; Powell, Costa, Lopes, & Vasconcelos, 2011), continued ant surveys at Agua Salud and in older forests are needed to understand the temporal dynamics of liana effects on the structure of arboreal ant communities. The results of this study concur with those of other studies showing that arboreal ant community structure changes during early succession, but it is unclear whether these patterns are driven by stand-level changes or by ontological changes within individual trees. Focused sampling of ants on a wide range of tree sizes and tree species distributed across successional stages would clarify the mechanisms underlying this pattern.

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DATA AVAILABILITY

Data available from the Dryad Digital Repository: [DOI](#) (Adams, Gora, et al., 2019).

Supporting Information

Filename	Description
btp12709-sup-0001-Supinfo.docx	Word document, 109.8 KB

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