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Strong influences of a dominant, ground-nesting ant on recruitment, and establishment of ant colonies and communities

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ABSTRACT

Many factors drive the organization of communities including environmental factors, dispersal abilities, and competition. In particular, ant communities have high levels of interspecific competition and dominance that may affect community assembly processes. We used a combination of surveys and nest supplementation experiments to examine effects of a dominant ground-nesting ant (*Pheidole synanthropica*) on (1) arboreal twig-nesting, (2) ground-foraging, and (3) coffee-foraging ant communities in coffee agroecosystems. We surveyed these communities in high- and low-density areas of *P. synanthropica* over 2 years. To test for effects on twig ant recruitment, we placed artificial nesting resources on coffee plants in areas with and without *P. synanthropica*. The first sampling period revealed differences in ant species composition on the ground, in coffee plants, and artificial nests between high- and low-density sites of *P. synanthropica*. High-density sites also had significantly lower recruitment of twig ants and had species-specific effects on twig ant species. Prior to the second survey period, abundance of *P. synanthropica* declined in the high-density sites, such that *P. synanthropica* densities no longer differed. Subsequent sampling revealed no difference in total recruitment of twig ants to artificial nests between treatments. Likewise, surveys of ground and coffee ants no longer showed significant differences in community composition. The results from the first experimental period, followed by survey results after the decline in *P. synanthropica* densities suggest that dominant ants can drive community assembly via both recruitment and establishment of colonies within the community.

Abstract in Spanish is available with online material.

Key words: artificial nest; coffee agroecosystem; colonization rate; community assembly; community structure; Mexico; nest-site limitation; *Pheidole synanthropica*.

THE STRUCTURE OF ECOLOGICAL COMMUNITIES AND COMMUNITY ASSEMBLY PROCESSES HAVE long fascinated ecologists (e.g., Perfecto 1994, Bell 2001, Hubbell 2001, Leibold *et al.* 2004, Chase 2005, Gotelli & McGill 2006), and interspecific competition is often considered an important factor influencing community organization. Indeed, many studies across terrestrial and aquatic systems with both vertebrates and invertebrates have found significant effects of competition in pair-wise interactions. However, evidence for interspecific competition as a key structuring factor of animal communities is inconclusive.

Several studies have found evidence in support of strong interspecific competition in communities (Room 1971, Connell 1983, Schoener 1983, Gurevitch *et al.* 1992). The removal of a dominant competitor had significant effects on community structure in marine sub-tidal communities (Dürr & Wahl 2004), coral reef communities (Chadwick & Morrow 2011), small mammal and marsupial communities (Valone & Brown 1995) as well as tropical butterfly communities (Kunte 2008). However, several other experiments—observational and review studies—indicate either a limited effect of competition or context dependency in alpine plant communities (Pavlov *et al.* 1998, Pierce *et al.* 2007), grasslands (Wilson & Tilman 1991) and ant communities (Cerdá *et al.* 1998, Floren & Linsenmair

2000, Retana & Cerdá 2000, Gibb & Hochuli 2004, Sanders *et al.* 2007, Baccaro *et al.* 2012).

Ants are useful organisms for testing hypotheses about community assembly and species co-existence (Palmer *et al.* 2000, Stanton *et al.* 2002, McGlynn 2006) as they are abundant, diverse, and represent a large fraction of tropical animal biomass (Hölldobler & Wilson 1990). Of the factors affecting ant community assembly, competition has long been considered to play an important role in determining community composition and structure (Leston 1978, Savolainen & Vepsäläinen 1988, Andersen 1992, Parr & Gibb 2010, Cerdá *et al.* 2013). The study of interspecific competition in ant communities as a whole, however, has placed a strong emphasis on competitive effects on richness and composition rather than on assembly processes. Species co-existence is related to the ability of a species to arrive and survive in a given community (Andersen 2008), yet most studies of competition and co-existence in ant communities examine only the survival phase, rather than colonization.

For a community of arboreal twig-nesting ants (hereafter, ‘twig ants’), nest takeovers are common and nest sites are often limiting, thus competition for nest sites is commonly inferred (Brian 1952, Yamaguchi 1992), and, in at least one case, is experimentally demonstrated (Palmer *et al.* 2000). Furthermore, competition between queens or individuals of budding colonies might limit the founding of new colonies (Stanton *et al.* 2002). Twig ants in coffee agroecosystems are nest-site limited (Philpott &

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Foster 2005), and face competition from other twig ants, canopy ants, and ground-nesting ants that may inhibit colonization and survival. Indeed, previous studies show that a dominant canopy ant can limit twig ant colonization, even without significant effects on species composition or richness (Philpott 2010).

We examined influences of a numerically dominant ground-nesting ant species, *Pheidole synanthropica*, on the recruitment and establishment of twig ants in coffee agroecosystems in Chiapas, Mexico, as well as impacts on the establishment of ground-foraging and coffee-foraging ant species. Specifically, we addressed the following questions: (1) are differences in the density of *P. synanthropica* related to differences in richness or species composition of ground-foraging ants, coffee-foraging ants, and twig ants? (2) Do differences in *P. synanthropica* density affect overall twig ant colonization success? (3) Does *P. synanthropica* have species-specific effects on twig ant colonization?

METHODS

STUDY SITE AND STUDY SYSTEM.—We conducted the study in Finca Irlanda, a 280-ha shaded coffee farm in the Soconusco region of Chiapas, Mexico. The farm is located between 900–1100 m asl and receives on average 5726 mm of rain annually. Approximately 50 species of shade trees provide 30–75 percent shade to the coffee bushes below.

The ground-nesting, dominant ant *P. synanthropica*, forms nests in the soil but forages both on the ground and in the coffee plants and frequently tends large-scale insect populations in coffee (Gonthier *et al.* 2013a). With a broad foraging capacity, this ant is often found among clusters of colonies that dominate expansive areas. *Pheidole synanthropica* is one of the most widely distributed ant species found in the coffee farm—recognized for both its competitive ability and pest-control potential (Gonthier *et al.* 2013b). Although this species is commonly found in disturbed areas and coffee farms, relatively little is known about its effects on other ants.

In addition to *P. synanthropica*, there are an estimated 107 ground-foraging, coffee-foraging, and twig ant species in the study region. Of these, 88 are ground-foraging ants (hereafter, ‘ground ants’), 55 are coffee-foraging ants (hereafter, ‘coffee ants’) and 40 are twig ant species (Philpott & Foster 2005, De la Mora *et al.* 2013). Twig ant species nest in dry, hollow coffee twigs still attached to coffee plants and also readily occupy artificial nests (Philpott & Foster 2005). As ecological communities are effectively determined by their sampling methods, we considered ground and coffee ants to be those species that are attracted to baits on the ground or on coffee plants, respectively. We define twig ants as those that are collected from dry coffee twigs or artificial nests placed on coffee plants. The three ant communities of interest in this study are not mutually exclusive. Some ants that nest in the ground and visit ground baits may also visit baits on coffee plants. Likewise, some twig ants are attracted to baits on coffee plants. We estimate that about 65 percent of the ground ant species (~58 species), 48 percent of the coffee ant species (~29 species), and 50 percent of the twig ants (~20

species) are unique to these defined communities. Prior work in this study system and in cacao agroecosystems suggests that baits capture at least 30 percent of the species encountered with passive surveys, such as mini-Winklers (Delabie *et al.* 2000, De la Mora *et al.* 2013). Although baits may not capture all species present, the efficiency of this method enables surveys at both greater resolution and greater extent (242 total baits in each site of 400 m²) that would not be feasible with passive methods (*i.e.*, pit-falls, mini-Winkler).

STUDY DESIGN.—To address our three primary questions we established six, 20 × 20 m sites, each separated by a minimum of 150 m (Fig S1). Three sites were randomly placed in areas with high *P. synanthropica* density and the three remaining sites we randomly placed in areas with low *P. synanthropica* density. To examine differences in species richness and community composition between high- and low-density sites for all the three ant communities (*e.g.*, ground, coffee, and twig ants), we used baiting methods (described below) and dry twig removal on coffee plants. To compare colonization rates and species-specific differences in twig ants between *P. synanthropica* sites, we added artificial nesting resources in the form of hollow bamboo twigs to coffee plants within each site.

ANT SAMPLING.—We surveyed ground and coffee ants in June 2012 and June 2013 (Table 1) with small amounts of canned tuna baits (5 g) every 2 m, for a total of 121 points in each site for both the coffee and ground communities. We placed baits for ground ants on the ground and baits for coffee ants were placed at eye level on the coffee bush closest to the ground bait. We surveyed the baits for ants found within 10 cm of the bait no more than 20 min after bait placement. Species occurrences at baits can be dominated by strong recruiting ant species and limit the observed occurrences of weaker species. However, small-scale time series of bait occupancy reveal that strong recruiter species require approx. 20 min to completely exclude and deter other species (*e.g.*, Perfecto 1994). On the basis of this, we checked baits within 20 min so that, on average, we assessed the baits prior to exclusion of weaker species by strong recruiter species.

Twig ant species were destructively surveyed in each of the sites in June 2012. All dry twigs of each coffee plant within each 20 × 20 m site were broken off and removed from the site. We recorded the total number of hollow twigs and occupied twigs, as well as the number and identity of all ant colonies found. For all ant surveys, we collected all individuals that could not be identified with certainty in the field and later identified them in the lab. All individuals were identified to species or to morphospecies.

To examine *P. synanthropica* impacts on twig ant colonization, we attached artificial nests made of hollow bamboo twigs to coffee branches at each site during two different time periods (Oct–Dec 2012 and Feb–May 2013). Every 5 m within the plot, we chose one coffee plant on which to add nests. We placed five artificial nests on coffee plants with twist ties 0.5–2.0 m above-ground for a total of 25 bushes and 125 bamboo nests per site, per sample period. The bamboo twigs (10–20 cm long with

TABLE 1. *Timeline of surveys and data collection.*

Dominant ant density differences in treatments	Month(s)	Activity
<i>Pheidole synanthropica</i> density significantly different in high- and low-density sites	June 2012	Survey 1—surveys of ground, coffee and twig-nesting ants
	October–December 2012	Sample 1—artificial nests placed and collected
<i>Pheidole synanthropica</i> density not different in high- and low-density sites	February–May 2013	Sample 2—artificial nests placed and collected
	June 2013	Survey 2—surveys of ground and coffee ants

3–8 mm diameter openings) were open at one end, and sealed at the other. Bamboo of this size was selected to best approximate size and variation in hollow coffee twigs. After 12 wk, we collected the nests and identified the colonizing species.

VEGETATION SAMPLING.—We conducted vegetation surveys to ensure that any shifts in the ant community in high- and low-density *P. synanthropica* sites were not due to concomitant changes in vegetation. In each site, we measured canopy cover, tree density, tree diversity, proportion of trees in the genus *Inga* and coffee plant density. We surveyed canopy cover twice (September 2012 and March 2013) with a convex spherical densiometer every 20 m within a 1-ha plot surrounding the survey sites (36 total measurements) and we used the mean values across the two sample periods for analysis. In 50 × 50 m plots surrounding ant survey sites, we counted the number of tree individuals, the number of tree species, and the percentage of trees in the genus *Inga*. *Inga* spp. trees are the most common type of shade tree planted in the region and reflect the management intensity of a coffee farm (*i.e.*, higher proportions of *Inga* indicate higher management intensity and less vegetation complexity). Within each ant survey site, we counted all coffee plants. We then combined all vegetation characteristics sampled in a vegetation complexity index (VCI). To calculate the VCI, we first scaled each individual vegetation characteristic by dividing all observed values by the largest observed value, such that every observed value for each characteristic fell on a scale from 0–1, where 1 signifies greater vegetation complexity. As coffee plant density and the proportion of trees in the genus *Inga* are generally negatively correlated with vegetation complexity, we subtracted the product from 1 so that higher coffee densities and proportions of *Inga* were closer to a value of zero. Then, values calculated for individual vegetation characteristics were averaged to obtain a single value between 0 (low vegetation complexity) and 1 (high vegetation complexity) for each site. To compare vegetation characteristics between high- and low *P. synanthropica* density sites, we used independent samples *t*-tests with a Bonferonni correction to account for multiple tests (one for each of the five vegetation characteristics and the VCI).

DATA ANALYSIS.—We compared ant richness and twig colonization rates with generalized linear models (GLM). We included richness of ground, coffee, and twig ants, and the proportion of artificial nest occupation as dependent variables. We fit richness variables with a Poisson distribution and the proportion of artificial nest occupation with a binomial distribution. The *P. synanthropica* density, survey year, the interaction of those terms we used as fixed effects (Table 2). *Pheidole synanthropica* density was a continuous (rather than categorical) variable in the analysis, and values were determined from the proportion of ground or coffee baits occupied by *P. synanthropica*. Non-significant fixed effects were removed to improve model fit.

We compared species composition of ants in high- and low *P. synanthropica* density sites for ground, coffee, twig, and artificial nest ants. Separate comparisons were conducted for the first and second sample and survey periods. We used non-metric multidimensional scaling (NMDS) to visualize differences in ant community composition and assessed statistical differences using permutational multivariate analysis of variance (PERMANOVA) and analysis of similarity (ANOSIM) with the Bray–Curtis distance matrix in the ‘vegan’ package in R (R Development Core Team 2013). PERMANOVA analysis compares the centroid values between groups, while ANOSIM compares the mean rank distance within groups to the mean rank distance between groups (Anderson & Walsh 2013).

We removed bait visits by *P. synanthropica* from the dataset prior to analyses so that differences in species composition are

TABLE 2. *Generalized linear model for effects of Pheidole synanthropica and survey/sample period on ground, coffee and twig ant richness as well as on artificial nest ant colonization rates.^a*

Dependent variable	Factors	χ -value	<i>P</i>
Ground ant richness	% <i>P. synanthropica</i> ground occupation	–1.976	0.048
	Survey period	0.295	0.768
	% <i>P. synanthropica</i> ground occupation × survey period	–	–
Coffee ant richness	% <i>P. synanthropica</i> coffee occupation	–4.852	0.005
	Survey period	–2.036	0.042
	% <i>P. synanthropica</i> coffee occupation × survey period	–	–
Twig-nesting ant richness	% <i>P. synanthropica</i> coffee occupation	–2.715	0.006
Artificial nest occupation	% <i>P. synanthropica</i> coffee occupation	–3.066	0.002
	Sample period	–3.042	0.002
	% <i>P. synanthropica</i> coffee occupation × sample period	–	–

^aHyphens indicate non-significant relationships that have been backward eliminated to improve model fit.

not attributed to differences in abundance of *P. synanthropica*. After removing *P. synanthropica*, however, the number of total ant bait visits between high- and low-density sites in the first year differed (coffee *t*-test: $t = 13.48$, $P = 0.0001$, ground *t*-test: $t = 5.66$, $P = 0.005$), thus we used presence/absence data at a site to limit the effect of removing *P. synanthropica* from the data. In the second year, the number of bait visitors was not different between high- and low-density sites in coffee surveys (*t*-test: $t = 1.42$, $P = 0.22$), but did differ in ground surveys (*t*-test: $t = 3.02$, $P = 0.039$).

To investigate differences in relative abundance of twig ant species between high- and low-density *P. synanthropica* sites, we compared the number of occupied hollow coffee twigs and artificial nests by individual species between high- and low *P. synanthropica* density sites using chi-squared tests. For this, we tested only those ant species found occupying a twig or artificial nest on six or more occasions (seven coffee twig species, 15 artificial nest species).

To examine the influences of vegetation characteristics on ant colonization, we regressed the proportion of occupied nests against each vegetation characteristic. We then used Pearson's correlations coefficients (r) with dimensions 1 and 2 of the NMDS as dependent variables and the six vegetation factors as independent variables.

RESULTS

PHEIDOLE SYNANTHROPICA DENSITY.—During the first sample period, *P. synanthropica* was much more abundant in high-density sites (Fig. 1), occupying 97.0 ± 3.7 (SE) percent of all coffee baits in high-density sites, but only 2.2 ± 2.2 percent in low-density sites ($t = 21.977$, $df = 2$, $P = 0.001$). Likewise, *P. synanthropica* occupied 82.9 ± 7.4 percent of all ground baits in high density but only 1.9 ± 1.5 percent in low-density sites ($t = 10.678$, $df = 2$, $P = 0.009$). The second sample period revealed dramatic declines in *P. synanthropica* density such that *P. synanthropica* density did not differ between high- and low-density sites. *Pheidole synanthropica* occupied 7.4 ± 7.4 percent of coffee baits and 9.3 ± 5.6 percent of ground baits in high-density sites and 0.9 ± 0.9 percent of coffee baits and 2.8 ± 1.6 percent of ground baits in the low-density sites (ground: $t = 0.69$, $df = 2$, $P = 0.56$; coffee: $t = 0.87$, $df = 2$, $P = 0.48$).

ANT SURVEYS.—There were 62 ant species collected across all assemblages and habitats. The most frequently encountered ground ants were *Pheidole protensa* (31.8% of baits) and *Solenopsis geminata* (22.4%). The most frequently encountered coffee ants were *Brachymyrmex* sp. 1 (7.6% of baits), *Azteca sericeasur* (5.2%) and *Pheidole* sp. 1 (4.6%). The most frequently encountered twig ants were *Pseudomyrmex simplex* (25.5% of occupied coffee twigs), followed by *Procrystocerus scabriusculus* (18.8%) and *Pseudomyrmex ejectus* (13.8%). There were overlaps in composition among the three assemblages; ground ants shared 14 species with coffee ants and coffee ants shared nine species with twig ants. Only *Solenopsis picea* occurred across all three assemblages.

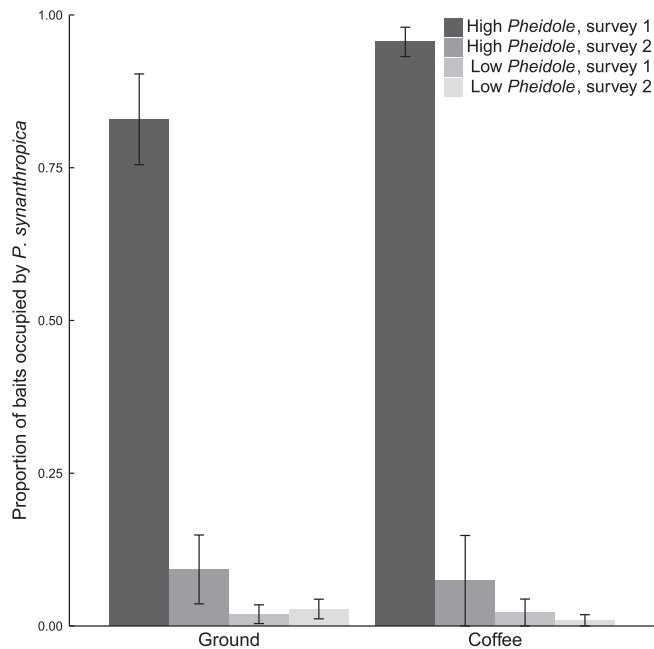


FIGURE 1. Average proportion of baits occupied by *P. synanthropica* in designated high- and low-density sites for both sampling years. For the first survey period, sites are significantly different, however, for the second survey period, the high-density sites in the second survey dropped and are not significantly different from low-density sites.

We sampled a total of 638 hollow twigs during the twig ant survey of which 431 were occupied. However, there was no difference in the number of hollow twigs ($t = 0.12$, $df = 2$, $P = 0.91$) between high- and low *P. synanthropica* density sites. Ant richness was significantly influenced by *P. synanthropica* density across ground, coffee and twig ant surveys (Table 2). While survey period was a significant factor in determining coffee ant richness; neither ground nor coffee ant richness responded to the interaction between *P. synanthropica* density and survey year.

Species composition of ground ants and coffee ants differed between high- and low-density *P. synanthropica* sites, but twig ant composition did not. Ground ant composition differed in high- and low-density *P. synanthropica* sites (Fig. 2A, ANOSIM: $R^2 = 0.6825$, $P < 0.001$; PERMANOVA: $F_{8,1} = 8.1174$, $P = 0.0002$). Ground ant species composition also differed between the first and second surveys (ANOSIM: $R^2 = 0.5167$, $P = 0.0021$; PERMANOVA: $F_{8,1} = 5.5383$, $P = 0.0004$). There was a significant interaction between *P. synanthropica* density and sample period (PERMANOVA, $F_{8,1} = 2.4206$, $P = 0.0419$) indicating that the difference between high- and low-density sites only existed during the first, but not second sample period. Coffee ant species composition (Fig. 2B, ANOSIM, $R^2 = 0.6106$, $P = 0.0037$; PERMANOVA, $F_{9,1} = 6.7184$, $P = 0.0001$) differed in high- and low-density *P. synanthropica* sites. As with the ground ants, coffee ant species composition also differed by survey period (ANOSIM: $R^2 = 0.3148$, $P = 0.039$, PERMANOVA:

$F_{9,1} = 3.1978$, $P = 0.0101$). However, there was no significant interaction between *P. synanthropica* density and sample period for coffee ant composition. Twig ant composition was similar in high- and low-density sites (Fig. 2C, ANOSIM, $R^2 = 0.1111$, $P = 0.2997$; PERMANOVA, $F_{4,1} = 1.5506$, $P = 0.20$). Twig ants were not resurveyed due to destructive sampling from the first survey, so we are unable to compare between survey periods.

ARTIFICIAL NEST COLONIZATION.—We recovered 1154 artificial nests: 555 (73.3% of those placed) from low-density *P. synanthropica* sites and 599 (80.5%) from high-density *P. synanthropica* sites. Of the recovered artificial nests, 479 were occupied (41.5%) by one of 29 ant species. The two most common ants in the artificial nests were *Pseudomyrmex gracilis* (24.6% of occupied nests) followed by *P. scabriusculus* (16.3%).

Artificial nest colonization differed with *P. synanthropica* density (Table 2, z -value = -3.066 , $P = 0.002$) and by sample period (z -value = -3.042 , $P = 0.002$). However, there was no significant interaction of *P. synanthropica* density and sample period, so the term was eliminated to improve model fit. Artificial nest occupation in low-density *P. synanthropica* sites was 55.5 percent greater than in high-density sites during the first sample period, but only 10.0 percent greater in the second sample period (Fig. 3A).

Species composition of ants occupying artificial nests strongly differed in high- and low-density sites (ANOSIM, $R^2 = 0.2981$, $P = 0.0153$; PERMANOVA, $F_{1,9} = 2.266$, $P = 0.019$), but there was no effect of sample period on composition (Fig. 3B, ANOSIM, $R^2 = 0.2981$, $P = 0.0153$; PERMANOVA, $F_{1,9} = 2.266$, $P = 0.019$). There was no significant interaction of *P. synanthropica* density with sample period (PERMANOVA: $F_{1,9} = 0.382$, $P = 0.947$).

SPECIES LEVEL EFFECTS.—The number of twigs occupied by particular ant species differed in the high- and low-density sites (Fig. 4A). In high *P. synanthropica* density sites, *P. scabriusculus* occurred more frequently than expected ($P = 0.0005$) while *Nesomyrmex echinatoidis* ($P = 0.0003$), *Myrmelachista mexicana* ($P = 0.0081$), *Pseudomyrmex elongatus* ($P = 0.0222$), and *P. ejectus*

($P = 0.0003$) all occurred less frequently than expected. The proportion of twigs occupied by other species did not differ with *P. synanthropica* density (*P. simplex*, $P = 0.075$; *Pseudomyrmex* PSW-53, $P = 0.061$).

Recruitment of particular species to the artificial nests significantly differed in sites with high- and low *P. synanthropica* density (Fig. 4B). Recruitment of *N. echinatoidis* ($P < 0.00001$) and *Camponotus striatus* ($P < 0.0001$) to artificial nests was lower in high *P. synanthropica* density sites. However, recruitment of *P. scabriusculus* ($P = 0.0002$) and *Cephalotes minutus* ($P = 0.0001$) was higher in high *P. synanthropica* density sites. Recruitment of other species did not differ with *P. synanthropica* density (*Camponotus brettesi*, $P = 0.281$; *Camponotus* sp. 1, $P = 0.770$; *Crematogaster carinata*, $P = 0.671$; *Crematogaster* sp. 1, $P = 0.159$; *Dolichoderus lutosus*, $P = 0.327$; *Neoponera crenata*, $P = 0.354$; *Pseudomyrmex elongatus*, $P = 0.743$; *P. gracilis*, $P = 0.832$; *Pseudomyrmex* PSW-06, $P = 0.925$; *Pseudomyrmex* PSW-53, $P = 0.313$; *Technomyrmex* sp. 1, $P = 0.471$).

VEGETATION AND ANT COLONIZATION AND COMPOSITION.—We found no vegetation differences in canopy cover, number of trees, number of tree species, percent of trees in the genus *Inga*, number of coffee plants, or the VCI between high- and low-density *P. synanthropica* sites (Table 3). Vegetation within the sites had some variable influence on ant groups (Table 3; Table S1). Ground ant richness negatively correlated with vegetation complexity and ground ant composition varied with the number of tree species. Twig and coffee ant composition varied with canopy cover and twig ant composition varied with number of trees. Artificial nest ant composition varied with the number of trees and the percent of trees in the genus *Inga*. No vegetation factors correlated with artificial nest colonization (Fig. S2).

DISCUSSION

Our results demonstrate that dominant ant species are important to three diverse and spatially distinct assemblages of ants co-occurring in the same habitat. Specifically, sites with high densities

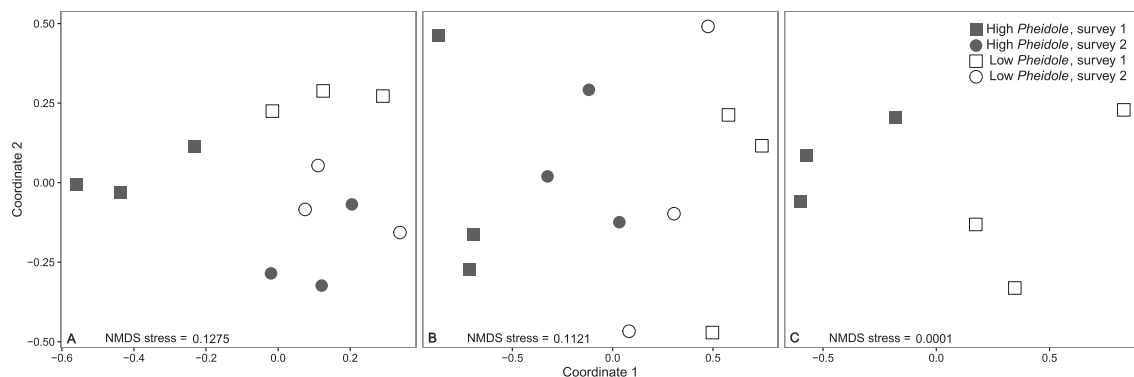


FIGURE 2. Non-metric multidimensional scaling plots comparing species composition of (A) ground, (B) coffee, and (C) twig-nesting ants in high- and low-density *P. synanthropica* sites. Analysis includes 2 years of survey data for (A) ground and (B) coffee ants; twig-nesting ants were surveyed destructively only once.

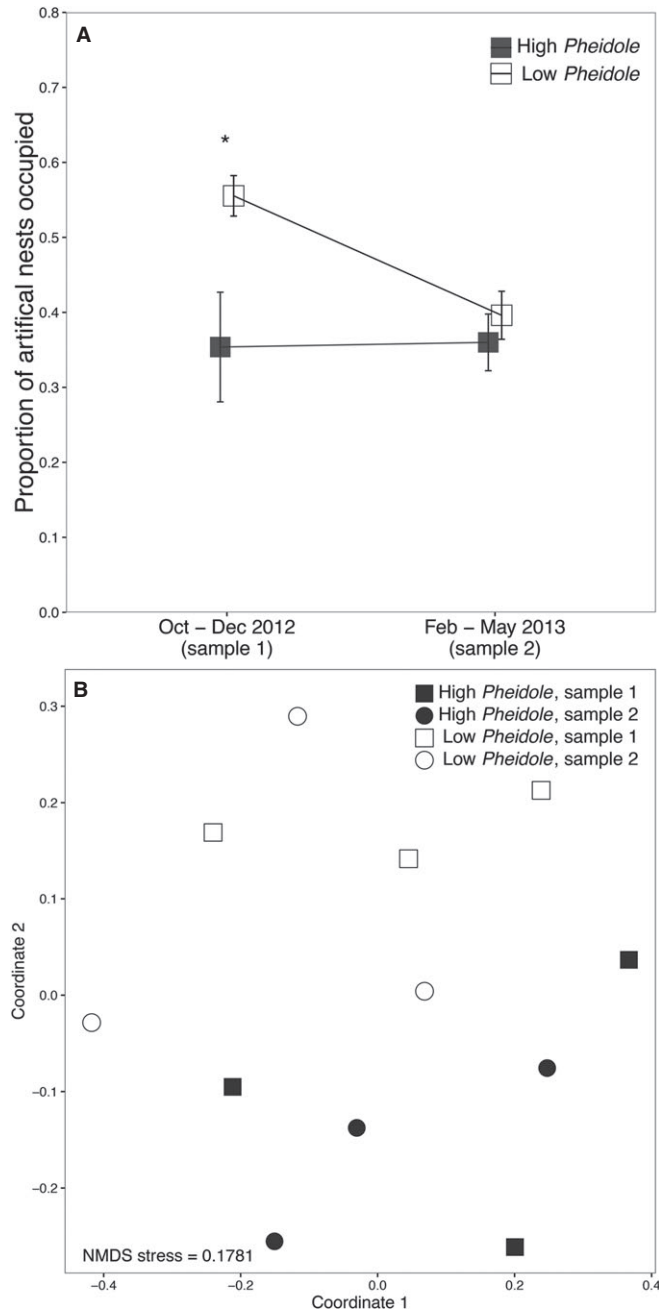


FIGURE 3. Results from artificial nest occupation experiment where (A) shows the proportion of artificial nests occupied by twig-nesting ants in high- and low *P. synanthropica* density sites across the two sample periods; (B) is the non-metric multidimensional scaling plot of ants found colonizing the artificial nests in both high- and low *P. synanthropica* density sites across both sample periods.

of the abundant, ground-nesting, ant *P. synanthropica* had fewer ant species and different ant community composition across the three groups measured (ground, coffee, and twig ants). Furthermore, overall colonization rates of arboreal twig-nesting species—an ant group with which *P. synanthropica* is not competing for nesting resources—was lower in sites with high densities of this dominant ant species. Furthermore, our study provides support that a dominant ant species may dictate community assemblage

processes due to lasting species-specific effects on colonization success. Thus, our study indicates that a dominant ant species may affect ant communities at both arrival and survival stages of colony recruitment.

During the course of our study, there was a dramatic drop in density of *P. synanthropica* in the high-density sites. Such a dramatic change in the presence of *P. synanthropica* in the selected areas of the farm is not a routine occurrence and, based on

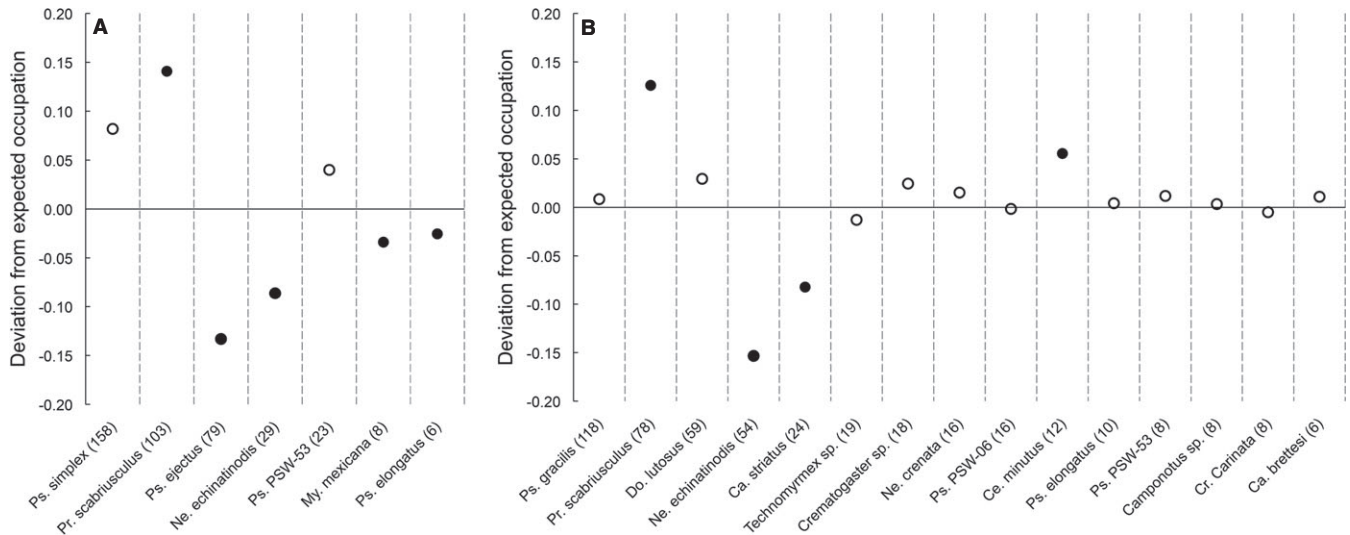


FIGURE 4. (A) Deviation from expected occupation of coffee twigs in high- and low-density *P. synanthropica* sites for the most abundant species found during twig ant surveys. Black points represent significant deviations from areas with low-densities of *P. synanthropica*. Points above the line indicate that more ant nests were found than expected with high densities of *P. synanthropica*. Numbers listed in parentheses beside species' names indicate the total number of nests found. (B) Deviation from expected occupation of artificial nests in high- and low-density *P. synanthropica* sites for the most abundant colonizing species. Black points represent significant deviations from areas with low densities of *P. synanthropica*. Points above the line indicate that more ant nests were found than expected with high densities of *P. synanthropica*. Numbers listed in parentheses beside species' names indicate the total number of nests found.

TABLE 3. Vegetation characteristics of coffee habitat in high- and low-density *Pheidole synanthropica* sites.^a

Vegetation characteristic	Sites with high <i>P. synanthropica</i> density	Sites with low <i>P. synanthropica</i> density	<i>t</i>	df	<i>P</i>
Canopy cover (%)	55.37 ± 8.29	47.37 ± 4.32	0.856	4	0.321
No. coffee plants	152.33 ± 42.53	165.33 ± 29.95	-0.25	4	0.405
No. trees	35.67 ± 5.36	26.33 ± 5.93	1.168	4	0.895
No. tree species	11.33 ± 1.33	9.67 ± 2.03	0.687	4	0.593
Percent of <i>Inga</i> spp. trees ^b	48.66 ± 14.86	42.63 ± 9.9	0.337	4	0.337
Vegetation complexity index	0.63 ± 0.08	0.55 ± 0.06	0.851	4	0.851

^aVegetation measured in 50 × 50 m plots. Numbers show mean ± SE.

^bPercent of total trees in the plot belonging to the genus *Inga*.

previous sampling, has not occurred for at least the 5 years prior to this study. In fact, annual studies of this ant from 2009–2012 indicated that areas dominated by *P. synanthropica* shift only moderately and are probably indicative of an ant mosaic—a phenomenon more commonly described for tropical arboreal ants (Perfecto & Vandermeer 2013). The decline in occurrence of *P. synanthropica* at baits coincided with a fungal epidemic of the coffee leaf rust disease (*Hemileia vastatrix*, Berkeley and Broome, 1869). This disease creates rust colored lesions on the coffee leaves, kills infected leaves that then dry out and fall to the ground, such that highly infected plants become nearly completely

defoliated. Subsequent to the outbreak of *H. vastatrix* (in January 2013), the farm workers applied large quantities of calcium carbonate to the soil (in February 2013) and pruned back many of the most severely damaged plants to 30 cm stumps that resprouted with the onset of the rains that begin in May. While the specific cause and exact timing of the population decline of *P. synanthropica* is unknown, it may be tied to the coffee leaf rust epidemic, the application of calcium carbonate (or other substances that may have been applied to control the outbreak), indirect losses of foraging habitat due to coffee leaf damage or some combination of effects.

Regardless of the exact cause of the declines of this dominant ground-nesting ant, it is interesting to consider the implications of this uncontrolled, natural experiment, and the ensuing drop in *P. synanthropica* density. Colonization of artificial nests and species composition for of all ants differed during the first sample period, but did not differ in the second sample period, corresponding to the lack of difference in *P. synanthropica* density in the two sites. However, it was colonization in low-density sites, rather than in high-density sites, that declined between sample periods. The decline in low-density sites may be a result of the same factor(s) driving decreases in *P. synanthropica* density, or may be similar to previously documented drops in twig ant nest colonization during the dry season (between December–April) in non-rust years (Philpott 2010). Yet, colonization rates in high-density sites remained consistent between the two sample periods. One possible explanation for the lack of a successive decline could be that twig ants in these sites were previously limited in colony expansion or budding, a common process for nest-site limited polydomous twig ants (Stanton *et al.* 2002), such that when the density

of *P. synanthropica* dropped, ant colonies in coffee twigs expanded to occupy artificial nests in those sites. It may be that twig ant species more commonly found with *P. synanthropica* are more resilient to coffee resource declines. Or, it may be that twig colonization did decline, but lagged behind the areas without *P. synanthropica*. Finally, although the study area as a whole experienced dramatic coffee defoliation, no significant drops in twig ant abundance were observed across the farm as a whole (S. Philpott, unpubl. data), providing further indication that factors other than vegetation differences are influencing the ant assembly processes.

The changes recorded in other ant species, particularly for the twig and coffee ants, are unlikely related to management effects. In part, this is because coffee and twig ants rarely forage on the ground and obtain most of their resources from the coffee plants, operating as ‘cryptic herbivores’ that primarily feed on nectar and honeydew (Davidson *et al.* 2003, Hunt 2003). These types of resources were likely just as abundant on the coffee plants before and after the application of calcium carbonate on the soil.

Furthermore, changes in *P. synanthropica* density occurred only in the three high-density sites, but all management activities, primarily the spread of calcium carbonate on the soil, was similar across all sites. If management was the driving factor in ant community changes, we would expect similar or proportional declines in ant richness in high- and low *P. synanthropica* sites between the two sample periods. Instead, species richness of coffee-foraging ants declined by 20 percent between sample periods in the low-density sites but increased by 180 percent in the high-density sites. For ground-foraging species, low-density sites experienced a 20 percent increase in species richness between survey periods, but the high-density sites experienced an even larger 50 percent increase. Changes in species richness of artificial nest ants between samples did not vary much (20 and 25 percent declines in low- and high-density sites, respectively), but changes in total recruitment did vary between sample periods (Fig. 3A). There are likely many factors that contribute to the results we found, but the findings of this study point to a relatively strong effect of dominant species on colonization and establishment of ant communities.

We see strong effects of *P. synanthropica* on species that represent three overlapping but distinct ant assemblages. The effects of *P. synanthropica* on ants could be either direct (*e.g.*, food competition, aggression to founding queens), or could be indirect via a competition cascade. Our colonization experiment with twig ants indicates that effects on species composition may be stronger at the recruitment stage of community assembly and persist through to colony establishment. This idea is supported by previous research on ant natural history and community assembly processes. Ants are social and adaptive organisms generally resilient to environmental stressors (Anderesen 1991). In part, this is because reproductive queens stay inside the nest and are thus physically insulated from exogenous threats and mortality rates after colonization are often low (Gordon & Kulig 1996). So while competitive effects do negatively affect colony growth and individual workers, it does

not ultimately induce mortality of the entire colony (Wiernasz & Cole 1995).

Recruitment is especially important in community assembly processes of sessile organisms (Schupp *et al.* 1989). As central place foragers, ants function similarly to sessile organisms, and therefore recruitment should strongly influence assembly processes in ant communities. Recruitment limitation leads to reduced ant density (Cole & Wiernasz 2002) and recruitment is enhanced with vegetative complexity (Philpott & Foster 2005). Perhaps most relevant to our study are findings that a different strong competitor (*Azteca sericeasur*, formerly called *A. instabilis*) also limits total ant recruitment (Philpott 2010). Our study builds on this and all past studies, showing that dominant species can limit overall recruitment and alter community composition with the effects that persist into establishment.

As with Philpott’s results (2010), ours show negative effects of the dominant competitor on species richness and a similar reduction—albeit a smaller and inconsistent effect—on total ant colonization. However, our findings differ in several important ways. First, *A. sericeasur* is an aggressive, behaviorally dominant, arboreal ant species. While it negatively affects species richness of arboreal twig-nesting ants, its effect on ground-foraging ant richness is actually positive (K. Ennis, unpubl. data). In contrast, *P. synanthropica* is a numerically dominant, ground-nesting species with broad negative effects on ant richness across different ant assemblages and foraging strata. Second, while *A. sericeasur* and *P. synanthropica* have species-specific negative effects, *P. synanthropica* also has significant positive effects on the recruitment of at least a few common twig ant species. Finally, *A. sericeasur* did not affect species composition of twig ants (Philpott 2010), while differences in *P. synanthropica* density were associated with altered species composition of ground, coffee, and twig ant species. Both *A. sericeasur* and *P. synanthropica* had negative effects on species richness and colonization (Philpott 2010), so the difference between the dominant species may be driven by the positive and negative (rather than solely negative) species-specific effects of *P. synanthropica* on other ants.

The study of interspecific competition in ant communities has a long history. Early research reported strong effects of dominant species (Room 1971, Jackson 1984, Davidson *et al.* 2007), but these studies have been criticized for lack of experimental manipulation (Gibb & Hochuli 2004). More recently other, more manipulative, studies have found muted effects of dominant species (Gibb & Hochuli 2004), but are likewise criticized for indirect effects associated with ant removal methodology and short study duration (Cerdá *et al.* 2013). We chose not to experimentally remove *P. synanthropica* due to concerns of the indirect effects of ant removal and due to the feasibility of removal. *Pheidole synanthropica* has a much higher colony density than many of the successful manipulative removal/exclusion studies (*i.e.*, Gibb & Hochuli 2004, King & Tschinkel 2006). Our studies of *P. synanthropica* indicate that it has a foraging range of about 1.5 m from the nest entrance. Given the size of our sites (400 m²) we estimate that at least 40 separate colonies existed within each high-density site. Locating the estimated 120 nest entrances

across the three high-density sites, eliminating and/or excluding all nests and maintaining the removal or exclusion of *P. synanthropica* over the course of a year exceeded the limits of this study. We did not consider ant removal methods involving pesticides, as pesticides are not permitted for use in organic coffee farms.

Our results differ from several other studies that found little or no effect of dominant ants on richness—manipulative and non-manipulative alike (Floren & Linsenmair 2000, Gibb & Hochuli 2004, Sanders *et al.* 2007, Baccaro *et al.* 2012). First, our study examined the effects of a single dominant ant species, rather than combined effects of several dominant ant species. This is relevant because, as the results of our study and that of Philpott (2010) indicate, dominant ants cannot be assumed to have similar community level effects. Second, the dominant species in this study had significant effects on the newly colonized ant group (*i.e.*, ants occupying artificial nests), lending greater support to the idea that the negative effect of *P. synanthropica* on ant richness is an effect of competitive exclusion at the population and community level during dispersal and recruitment rather than simply an effect on individual ants.

In sum, this study suggests that competitive interactions from a dominant species at the recruitment phase may influence long-term community assemblage and structure, and that these effects can apply to several assemblages with variable resource requirements. However, effects of dominant species vary considerably in this respect, so the predictive nature of these relationships and their effects on communities cannot be assumed.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

FIGURE S1. Map of 20 × 20 m sites within the 45 ha plot.

FIGURE S2. Percent artificial nest occupation versus vegetation factors.

TABLE S1. *Pearson's correlation results corresponding changes in ant community characteristics with vegetation factors measured in study plots.*

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