Research

Oikos 119: 1954–1960, 2010
doi: 10.1111/j.1600-0706.2010.18430.x

Subject Editor: Bradford Hawkins. Accepted 20 April 2010

A canopy dominant ant affects twig-nesting ant assembly in coffee agroecosystems

Stacy M. Philpott

S. M. Philpott (stacy.philpott@utoledo.edu), Dept of Environmental Sciences, Univ. of Toledo, 2801 W. Bancroft St., Toledo, OH 43606, USA.

One commonly studied driver of community assembly is the effect of dominant species on subordinate species. Dominant species may impact community assembly during competitive sorting, or recruitment. For ants, important and abundant species in the tropics, several factors may drive community assembly including competition, dispersal, priority effects, and environmental conditions. Although competition is a hallmark of ant ecology, few have examined the influence of patchily distributed dominant ants on other ant species and diversity, especially at the recruitment stage. Here, I consider the impacts of a canopy dominant ant species, *Azteca instabilis*, and changes in vegetation on twig-nesting ant colony founding and ant community assembly in a coffee agroecosystem. I added artificial nests to coffee plants in areas with and without *A. instabilis* four times over a year, and then examined the occupation rate and identity of species colonizing nests. I also examined vegetation characteristics of sites where nests were added. The presence of *A. instabilis* on coffee plants drastically lowered colonization rates, but nest occupation increased with tree density, and with decreasing proportion of *Inga* spp. trees in the canopy. The presence of *A. instabilis* limited the number of nests occupied by six of the ten most common species; most rare species, however, were not affected by *A. instabilis* presence. Richness of colonizing ants in areas with *A. instabilis* was lower, but these effects did not significantly affect richness across broader scales. Despite large effects on individual species, species composition did not differ greatly in areas with and without *A. instabilis*, but some vegetation characteristics (basal area and tree richness) were predictive of ant composition. These results suggest that *A. instabilis* strongly affects founding events especially for common twig-nesting species and that both vegetation and influences from this dominant species affect community assembly of twig-nesting ants at the local scale.

One fundamental goal of ecology is to understand the structure and maintenance of diverse tropical assemblages. Since the classic work of Paine (1966), it has become common to consider antagonistic species as important factors in the community assembly process (Holt 1984, Forsman et al. 2001, Kneitel and Chase 2004, Wootton 2004). Although many studies consider the effects of predators, dominant competitors may also play important roles in community assembly of subordinates. First, dominant species may impact competitive interactions of subordinate species, thereby affecting species sorting. Communities where such interactions drive assembly have been referred to as dominance-controlled communities (Yodzis 1978). Additionally, dominant species may affect colony founding or colonization processes of subordinate species in communities. Founder-controlled communities, in contrast to dominance-controlled communities, are largely assembled via historical effects and dispersal abilities, in other words, stochastic factors (Yodzis 1978, Chesson and Warner 1981, Hubbell and Foster 1986). Those species arriving first in an area will come to dominate locally. However, if dominant species prevent subordinates from colonizing, than they may affect community assembly both via founding processes and competitive interactions.

Ants make ideal organisms for testing hypotheses about community assembly and species co-existence (Stanton et al. 2002, Palmer et al. 2003, Sanders et al. 2003, McGlynn 2006, Dunn et al. 2007). Ants are ubiquitous and diverse; in tropical ecosystems ants represent up to 80% of animal biomass (Hölldobler and Wilson 1990). Several factors likely contribute to assembly processes for ants (Palmer et al. 2003, Andersen 2008). Ant community assembly and ant diversity is influenced by differences in vegetation and habitat characteristics (Kaspari and Weiser 2000, Albrecht and Gotelli 2001, Ribas et al. 2003). Changes in vegetation characteristics may affect temperature or moisture conditions, thereby affecting ants (Nestel and Dickschen 1990, Perfecto and Vandermeer 1996, Kaspari and Weiser 2000). Changes to overstory vegetation may directly influence types and sizes of nests available to both arboreal and leaf litter ants (Torres and Snelling 1997, Armbrecht et al. 2004). Ants in less vegetatively complex habitats are sometimes nest-site limited due to low availability or variety of available nest sites (Armbrecht et al. 2004, Philpott and Foster 2005). Vegetation changes may also indirectly affect food availability and distribution – factors known to influence ant assembly (Kaspari et al. 2000, Blüthgen et al.

2004). Nonetheless, ant communities, in general, are often categorized as dominance-controlled communities, and competition is a 'hallmark of ant community ecology' (Hölldobler and Wilson 1990, Parr and Gibb 2010). Several studies have documented that interspecific competition from native or invasive ants affects ant communities (Leston 1978, Savolainen and Vepsäläinen 1988, Holway et al. 2002, Parr and Gibb 2010). Among the areas of ant community assembly that have received little attention, however, include a) processes acting at the recruitment stage and b) the influence of patchily distributed dominant ants on other ant species and diversity (Andersen 2008). Dominant species may strongly affect assembly, both in tropical assemblages, and in communities dominated by invasive ants (Sanders et al. 2007). Further, it has been hypothesized that dominant ants, when patchily distributed, create gaps into which subordinate species may colonize (Andersen 2008). One consideration linking both vegetation and competitive influences on ant assembly is that competitive hierarchies may change due to changes in environmental conditions (Cerda et al. 1997).

Here I test the hypothesis that the presence of a widespread behavioral dominant ant shapes local community composition at the colonization phase. Specifically, I examined the impact of an aggressive dominant canopy ant, *Azteca instabilis* on the assembly of twig-nesting ant communities in the understory of a coffee agroecosystem. *Azteca instabilis* is a canopy dominant that is a key player in several trophic interactions within coffee agroecosystems (Perfecto and Vandermeer 2008, Vandermeer et al. 2008). Further, *A. instabilis* is patchy within coffee agroecosystems (Vandermeer et al. 2008) – a pattern that may create opportunities for subordinate species to co-occur with *A. instabilis*. There are ~40 twig-nesting species in the community, and 7–10 species that are abundant enough to be considered potentially dominant. The founding process for twig-nesting ants is by occupation of nesting sites. I investigated whether the dominant species, *A. instabilis*, would affect community structure of twig-nesting ants at the nest founding stage. I studied the impact of *A. instabilis* on twig-nesting ants at both the within-patch level, and at the level of a 45 ha plot in a tropical coffee agroecosystem by examining the following hypotheses: 1) *A. instabilis* affects the abilities of twig-nesting ants to colonize artificial nest sites, 2) *A. instabilis* has disproportionate effects on certain twig-nesting ant species, and 3) *A. instabilis* affects patterns of species richness and species composition of ants colonizing artificial nests. Because vegetation characteristics affect ant diversity, and because *A. instabilis* locations were not manipulated, I also examined whether characteristics of the shade canopy over coffee plants differed in areas with and without *A. instabilis*, and whether any differences in twig-nesting ant colonization patterns relate to vegetation differences, and whether vegetation differences affected the composition of twig-nesting ant species colonizing artificial nests.

Methods

I worked in Finca Irlanda, a large (300 ha), organic, shaded coffee farm in Chiapas, Mexico (15°11'N, 92°20'W). The farm is located between 950–1150 m elevation, and receives ca 4500 mm of rain annually. There are at least 100 shade tree species on the farm that provide between 60–90% canopy cover over the coffee, but the canopy is dominated by *Inga* spp. *Azteca instabilis* ants nest in the shade trees and forage in nearby coffee trees thereby forming large patches of *A. instabilis* dominance (Vandermeer et al. 2008). More than 60 other arboreal ant species occur in the farm including other numerical dominants (*Camponotus textor*, *C. novogranadensis* and *Crematogaster* spp.) and twig-nesting species (*Pseudomyrmex* spp., *Cephalotes* sp., *Nesomyrmex* spp., *Procryptocerus* spp.) that inhabit hollow dry coffee twigs and canopy branches (Philpott and Foster 2005, Philpott et al. 2006).

To examine the influences of *A. instabilis* on twig-nesting ant establishment, I placed artificial nests (bamboo twigs) on coffee plants in areas with and without *A. instabilis*. In 2004, a 45 ha plot was established that has been surveyed several times for *A. instabilis* nests in the canopy trees (Vandermeer et al. 2008). I haphazardly chose four large *A. instabilis* colonies distributed throughout a 45 ha plot, and paired these with areas between 65–100 m away that did not have an *A. instabilis* colony. In each of the eight areas I selected eight coffee plants near to the canopy tree with the *A. instabilis* nest, and with high ant activity, or nearest to a focal tree. To limit nest expansion (e.g. budding) from natural nests on the coffee plants into artificial nests, I removed all potential natural nest sites by breaking off all dry twigs on coffee plants where artificial nests were added. Then, four times during one year (July 2006, October 2006, February 2007 and May 2007), I attached five artificial bamboo nests to each coffee plant with twist ties, along coffee branches 0.5–2.0 m above ground. The bamboo twigs (10–20 cm long with 3–8 mm diameter openings) were open at one end, and sealed at the other. I selected bamboo of this size to best approximate size and variation in hollow coffee twigs. Artificial nests remained for three months and were collected in September 2006, January 2007, April 2007 and July 2007. I recorded the number of bamboo twigs recovered, the number occupied by ants, and identified all ants found. I defined occupied nests as those bamboo twigs containing workers, brood or alates. Total sample sizes for each treatment (with and without *A. instabilis*) were four areas, 32 coffee plants, and 160 nests, across four sample periods for a total of 640 nests.

To examine whether presence of *A. instabilis* on coffee plants influences colonization by twig-nesting ants, I compared the proportion of occupied nests in areas with and without *A. instabilis* with univariate ANOVA with area as the replicate ($n = 4$), and *A. instabilis* presence and nest collection month as main factors. Within each area, for each sample date, the number of occupied and unoccupied nests on all coffee plants were summed before calculating the proportion occupied.

To examine influences of *A. instabilis* on individual ant species, I examined the number of occupied nests of each species in areas with and without *A. instabilis* using chi-square tests. To compare the mean number of individuals (workers plus brood) per colony in areas with and without *A. instabilis*, I used a nested ANOVA where colonies were nested within area. Colonies collected on different dates were treated as independent replicates. I defined colonies as all occupied nests of one species on one coffee plant during each time period. Number of individuals per colony was used as a metric to examine the influence of *A. instabilis* on success of nest establishment of twig-nesting species.

I examined twig-nesting ant species richness and composition in areas with and without *A. instabilis*. I compared mean species richness with a paired t-test. I also examined total observed (Mao Tao) and estimated richness (Chao2) across all areas with and without *A. instabilis* using species accumulation curves with EstimateS ver. 7.5 (Colwell 2005). I examined differences in species composition in three ways. First, I used non-metric multidimensional scaling (NMDS) and analysis of similarities (ANOSIM) with PAST (Hämmer et al. 2001) to visually and statistically compare species composition. ANOSIM produces a global p-value, as well as pair-wise comparisons, to indicate dissimilarity in species composition between treatments. Second, to look at the potential impacts of *A. instabilis* on the twig-nesting ant community at a larger scale, I examined species similarity among areas with *A. instabilis* and among areas without *A. instabilis*. I calculated similarity indices (Bray–Curtis and Jaccard) among areas with or without *A. instabilis* and compared mean values with independent samples t-tests. Third, I used a NPMANOVA with PAST (Hämmer et al. 2001) to examine the relative differences in communities among areas with *A. instabilis* and without *A. instabilis*. For the NMDS and NPMANOVA, I used Bray–Curtis as the similarity measure, and considered each area a replicate. Ants were not obtained for identification from three occupied nests, and these ants were not included in the species richness or composition analysis.

Vegetation characteristics of coffee habitats are widely variable, and may potentially affect twig-nesting ant colonization. In addition, because presence of *A. instabilis* was not directly manipulated, I wanted to ensure that any observed differences in colonization in areas with and without *A. instabilis* were not due to vegetation differences. I compared vegetation in 50 × 50 m plots surrounding each plot. I recorded the number of trees, number of tree species, and proportion of *Inga* spp. trees. I also measured the tree circumference and used data to calculate stand basal area for each plot (m^2 per hectare). To compare vegetation characteristics in areas with and without *A. instabilis*, I used paired t-tests and used a Bonferroni correction for multiple tests. To examine for influences of vegetation characteristics on twig-nesting ant colonization, I correlated artificial nest occupation with each of the four different vegetation characteristics measured using simple linear regressions. Finally, to examine the effects of the vegetation on the composition of twig-nesting ants, I used multiple regressions with dimensions 1 and 2 of the NMDS as dependent variables, and the four vegetation variables as independent variables.

Table 1. List of ant species found in artificial nests in areas with and without a canopy dominant ant. Numbers show numbers of colonized nests in each area.

Ant species	Without *A. instabilis*	With *A. instabilis*
Azteca instabilis	0	3
Brachymyrmex sp. 1	2	1
Camponotus (Colobopsis) sp. 1	5	2
Camponotus abditus	1	0
Camponotus striatus	2	0
Crematogaster sp. 1	2	0
Crematogaster carinata	8	0
Dolichoderus lutosus	21	5
Gnamptogenys sp. 1	1	0
Hypoponera sp. 1	2	1
Myrmelachista mexicana	1	0
Nesomyrmex echinatinodis	31	2
Pachycondyla sp. 1	5	1
Pheidole sp. 1	0	1
Procryptocerus hyleaus	57	29
Pseudomyrmex ejectus	11	18
Pseudomyrmex elongatus	10	8
Pseudomyrmex gracilis	8	3
Pseudomyrmex occulatus	1	1
Pseudomyrmex PSW-53	2	2
Pseudomyrmex simplex	40	25
Pseudomyrmex spiculus	0	2
Solenopsis sp. 1	0	1
Solenopsis picea	13	5
Tapinoma sp.	3	0
Technomyrmex sp. 1	1	0

Results

I recovered 604 bamboo nest sites from areas without *A. instabilis* (94% of those placed), and 561 bamboo nest sites from areas with *A. instabilis* (88% of those placed). Overall, 342 bamboo nests were occupied (29.4% of the total) by 26 ant species (Table 1). Presence of *A. instabilis* significantly limited artificial nest colonization by twig-nesting ant species (Fig. 1). For each time period, between 43% and 54% more nests were occupied in areas without *A. instabilis* ($F_{1,24} = 7.397$, $p = 0.012$). There were no differences in nest colonization by month ($F_{3,24} = 1.146$, $p = 0.351$) nor did the effects of *A. instabilis* on nest colonization differ with month ($F_{3,24} = 0.097$, $p = 0.961$).

There were some significant impacts of *A. instabilis* presence on colonization by particular species (Fig. 2a–b), but *A. instabilis* presence did not affect the numbers of individuals in colonies. Of the ten most common species, six

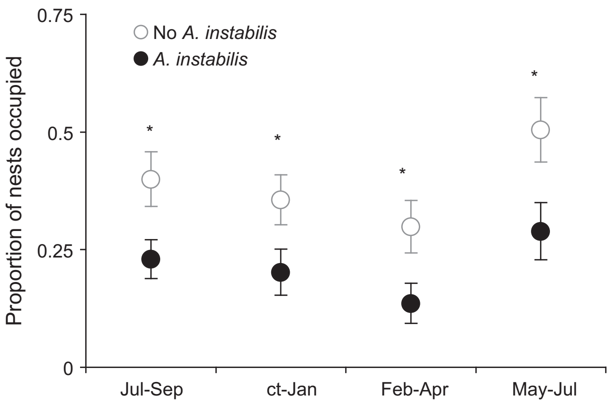

Figure 1. Proportion of artificial twig nests occupied by arboreal twig nesting ants in coffee plants in areas with or without *Azteca instabilis*. Asterisks indicate significant differences ($p < 0.05$) in occupation in areas with and without *A. instabilis*.

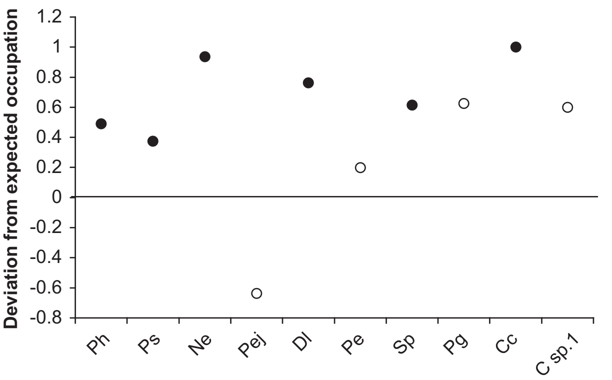

Figure 2. Deviation from expected colonization of *A. instabilis* areas for the 10 most common twig-nesting ant species. Black points show species that occupied significantly more nests in areas without *A. instabilis*. The line represents the point where species would have equally occupied areas with and without *A. instabilis*. Abbreviations are as follows: Ph = *Procryptocerus hyleaus*, Ps = *Pseudomyrmex simplex*, Ne = *Nesomyrmex echinatinodis*, Pej = *Pseudomyrmex ejectus*, Dl = *Dolichoderus lutosus*, Pe = *Pseudomyrmex elongatus*, Sp = *Solenopsis picea*, Pg = *Pseudomyrmex gracilis*, Cc = *Crematogaster carinata*, C sp. 1 = *Camponotus* (*Colobopsis*) sp. 1.

species colonized significantly (or nearly so) more nests in areas without *A. instabilis* (*Procryptocerus hylaeus*, p = 0.003; *Pseudomyrmex simplex*, p = 0.063; *Nesomyrmex echinatinodis*, $p < 0.001$; *Dolichoderus lutosus*, p = 0.002; *Solenopsis picea*, p = 0.059; *Crematogaster carinata*, p = 0.004). The number of colonized nests of the other four most common species did not differ with *A. instabilis* presence (*Pseudomyrmex ejectus*, p = 0.194; *Pseudomyrmex elongatus*, p = 0.637; *Pseudomyrmex gracilis*, p = 0.132; *Camponotus* (*Colobopis*) sp. 1, p = 0.257). Of the remaining 16 species, seven species were found only on plants without *A. instabilis*, and four were found only on plants with *A. instabilis*. Of the eight twig-nesting species for which colony size could be compared, numbers of individuals per colony did not differ in areas with and without *A. instabilis* ($p > 0.05$).

Azteca instabilis presence significantly affected ant richness at the local level but did not affect species composition. Mean observed species richness in areas with *A. instabilis* (8.25 ± 0.63 (SE)) was significantly lower than richness in areas without *A. instabilis* (12 ± 1.08) (t = 3.0, DF = 6, p = 0.024). The composition of species found colonizing areas with and without *A. instabilis*, however, did not significantly differ (Fig. 3). Visually, ant composition appeared similar in areas with and without *A. instabilis* (NMDS stress = 0.1431), and species composition did not significantly differ (ANOSIM, p = 0.6593).

The effects of *A. instabilis* on the twig-nesting ant community at the local level did not affect cumulative richness across all study areas. Species accumulation curves did not show differences in total observed or estimated species richness with and without *A. instabilis* (Fig. 4a–b). Species similarity within treatment areas did not differ. Bray–Curtis values among areas with *A. instabilis* (0.312 ± 0.022) did not differ from species similarity among areas without *A. instabilis* (0.436 ± 0.045) (t = 1.31, DF = 10, p = 0.220). Likewise, Jaccard values among plots with *A. instabilis* (0.311 ± 0.039) were similar to those among plots without *A. instabilis* (0.403 ± 0.036) (t = 1.22, DF = 10, p = 0.249). According to the 95% confidence ellipses of the NMDS (unpubl.), it appeared that composition in areas with *A. instabilis* was more variable than in areas without *A. instabilis*. However, there was no statistical difference in the scatter of points among areas with *A. instabilis* and areas without *A. instabilis* (NPMANOVA, F = 0.6905, p = 0.714) indicating that composition was not more or less variable in areas with *A. instabilis*.

Vegetation characteristics influenced twig-nesting ants, but did not account for differences in areas with and without *A. instabilis* (Table 2). The proportion of occupied nests significantly increased with tree density in a given area ($R^2 = 0.585$, $y = 76.843x + 41.921$, p = 0.027) and decreased with increasing proportion of *Inga* spp. trees ($R^2 = 0.6354$, $y = -0.7879x + 0.7801$, p = 0.018). Furthermore, there were some significant impacts of the vegetation on the species composition of ants colonizing the artificial nests (Table 3). Both basal area and tree species richness were significant predictors of NMDS dimension 2, demonstrating that vegetation factors related to ant composition in artificial nests. However, there were no differences in the vegetation of areas with and without *A. instabilis* (Table 2). Tree density, tree richness, stand basal area and the proportion of *Inga* spp. trees per plot did not differ in areas with and without *A. instabilis*.

Discussion

The results presented here show that both characteristics pertaining to the surrounding environment and the presence of dominant ant species are important for structuring the twig-nesting ant community at the colony founding stage. Here, tree density and lower *Inga* spp. densities correlated with increased nest occupation. Furthermore, basal area and species richness were predictive of some aspects of the ant species composition in artificial nests. Previous studies on both arboreal and litter twig-nesting ants in coffee

Table 2. Vegetation characteristics of coffee habitat in areas with and without *Azteca instabilis*.‡

Vegetation variable measured	Areas with *A. instabilis*	Areas without *A. instabilis*	t	DF	p
Stand basal area ($m^2\ ha^{-1}$)	13.06 ± 2.54	12.51 ± 0.77	–1.69	3	0.877
No. of tree individuals	53.25 ± 4.59	75.25 ± 8.89	1.781	3	0.173
No. of tree species	11.00 ± 0.91	12.50 ± 0.50	1.732	3	0.182
Percent of *Inga* spp. trees‡‡	62.10 ± 0.04	48.05 ± 0.24	1.345	3	0.271

‡vegetation measured in 50 × 50 m plots. Numbers show mean ± SE.
‡‡% of total trees in the plot belonging to the genus *Inga*.

Table 3. Regression between NMDS of ant composition and vegetation characteristics.‡

	DF	F	R^2	Stand basal area (m^2 ha^{-1})	No. of tree individuals	No. of tree species	Percent of *Inga* spp. trees‡‡
Dimension 1	4	0.740	0.623	0.586	–1.049	–0.487	0.236
Dimension 2	4	0.956	0.023	6.753**	–0.848	5.928*	2.069

‡numbers for individual vegetation factors are t-stats.
‡‡% of total trees in the plot belonging to the genus *Inga*.
$^{*}p < 0.05$, $^{**}p < 0.001$.

agroecosystems report that occupation of artificial nests increases in vegetatively complex farms with higher density and diversity of trees and diversity of nesting materials (Armbrecht et al. 2004, Philpott and Foster 2005). Similarly, environmental factors, such as leaf-litter depth, affect twig-nest colonization (Byrne 1994, Carvalho and Vasconcelos 1999). Importantly, however, none of the vegetation characteristics measured (basal area, tree density, tree richness, proportion of tree individuals belonging to the genus *Inga*) varied between areas with and without *Azteca instabilis*, so changes in the vegetation were unlikely to be driving the observed differences with presence of this competitive dominant.

There were several changes in abundance of particular species among areas with and without *A. instabilis*. There were fewer occupied nests in areas with *A. instabilis*. Further, *A. instabilis* negatively affected nest establishment of several common twig-nesting species, but did not affect the 16 rare species. One hypothesis to explain differences in effects on rare and common species could be that common species are more frequently polydomous than the rare species. Some twig-nesting ant species occupy several nest sites per plant usually assumed to comprise one colony (Frederickson 2006). The most common twig nesting species collected here frequently occupied multiple nests per plant (on 25.9% of plants where found). The rare species were less frequently polydomous (on only 16.5% of plants found). A second hypothesis is that rare twig-nesting species face competition from *A. instabilis* and from common twig-nesting species. Some common twig-nesting species were more abundant in non-*A. instabilis* areas, thus rare twig-nesting species may face 'compensatory interference' (Andersen and Patel 1994) such that they are limited in areas with and without *A. instabilis*. Presence of twig nesting ants in areas where artificial nests were placed did not influence colonization rates for ground-nesting ants (Byrne 1994). However, in lowland forests in Costa Rica, only an estimated 6.4% of nests are occupied at any given time (Byrne 1994), in contrast to between 55–85%

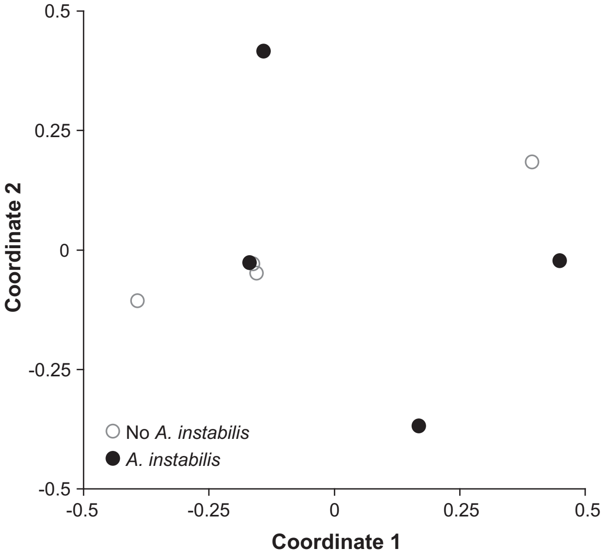

Figure 3. Non-metric multidimensional scaling analysis for twig-nesting ant community similarity for four areas with and four areas without *A. instabilis*. Each point represents the species found up to 160 artificial nests placed on coffee bushes. Open symbols show composition in areas without *A. instabilis*, closed symbols show composition in areas with *A. instabilis*.

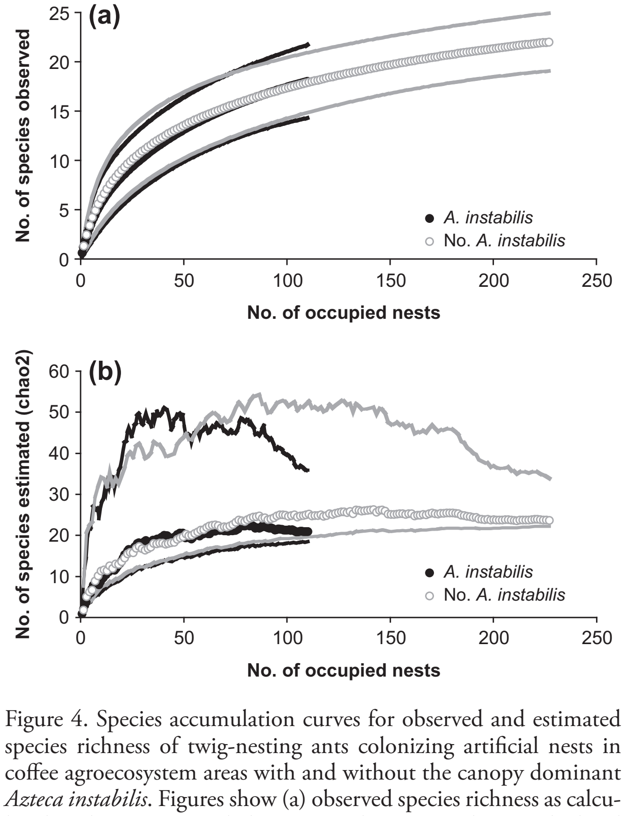

Figure 4. Species accumulation curves for observed and estimated species richness of twig-nesting ants colonizing artificial nests in coffee agroecosystem areas with and without the canopy dominant *Azteca instabilis*. Figures show (a) observed species richness as calculated with MaoTao and (b) estimated species richness calculated using the Chao2 estimator in EstimateS 8.0. Species found in areas with *A. instabilis* are shown with black circles, and in areas without *A. instabilis* in open circles. Lines show 95% CI for observed or estimated richness for symbols of the same color.

occupation of natural nests in dry coffee twigs in the study sites (Philpott and Foster 2005, Philpott unpubl.). Finally, it is possible that species rarity affected the ability to detect significant differences because of lowered statistical power.

Why did *A. instabilis* affect colonization of some common ant species, but not others? Of the ten most common species, six were less common and four were not more or less common in areas with *A. instabilis*. Differences in behavior and life history may enhance the abilities of some species avoid *A. instabilis* attacks. For example, *C.* (*Colobopsis*) sp. 1 queens have large phragmotic heads (Longino 2009). These large heads that often act as doors to twig-nests and could protect founding queens from *A. instabilis* attacks. Temporal differences in foraging times may also have facilitated nest colonization. Little is known about the temporal foraging patterns of most of the twig-nesting species, or specifically of the queens, but *A. instabilis* activity is significantly higher during the night than at the day (A. De la Mora pers. comm.). Diurnal foraging twig-nesting ants may have more successfully colonized. Further, large body size could provide protection from *A. instabilis* – however, two larger ants were less frequently found with *A. instabilis* (*P. hylaeus, D. lutosus*), and two were not affected by *A. instabilis* presence (*P. gracilis*, *C.* (*Colobopsis*) sp. 1). None of the species that were less common in *A. instabilis* areas are particularly aggressive species. In contrast, *Pseudomyrmex* spp., three of which were not affected by *A. instabilis*, do have well developed stings that may have defended them from *A. instabilis* attacks (Janzen 1967). Most of the species that were less common in *A. instabilis* areas are polygynous, whereas those species not affected by *A. instabilis* presence (e.g. *Pseudomyrmex* spp.) are likely not polygynous (G. Livingston pers. comm.). The mechanism of how polygyny would give some species an advantage is not obvious. Most of the common species encountered are polydomous (Longino 2009) but there are no obvious differences in colony size or proportion of alates for those species affected by *A. instabilis* (Livingston and Philpott unpubl.). In addition to direct aggressive effects that *A. instabilis* may have on colonizing queens, *A. instabilis* may indirectly influence colony founding by reducing the supply of food resources available to twig-nesting ants. Most common twig-nesting species, like *A. instabilis*, are generalist predators and tend hemipterans, but not enough is known about the specific diet requirements of the species to fully explore details of food competition between *A. instabilis* and twig-nesting ants (Longino 2009). Finally, *A. instabilis* presence may affect the local pool of ants available to colonize the nest sites, and future research could investigate the relative importance of dispersal and recruitment to areas with and without *A. instabilis*.

The dominant *A. instabilis* also affected the twig-nesting ant community, but effects differed with spatial scale. There were more species of ants in patches without *A. instabilis* compared with patches with *A. instabilis*, but these local effects on ant richness did not scale up to affect richness at a larger scale. Cumulative species richness across all areas with or without *A. instabilis* did not differ. However, species similarity did not differ statistically, and species composition was not more variable among areas with *A. instabilis*. That said, this study only incorporated four areas with and four areas without *A. instabilis*. Studies examining the larger-scale impacts of dominant ants are rare, even for studies examining competitive interactions. Although several studies have documented effects of dominant ants on the 'momentary' diversity of subordinate ants at baits (Parr and Gibb 2010), there are few tests of how the local effects scale up to affect entire assemblages. One study in S. African savanna habitats found that high abundance of dominant ants lowered richness of subordinate ants at baits and in pitfall traps, which is more indicative of assembly-level impacts (Parr 2008).

The effects of *A. instabilis* on nest colonization may be especially important for communities that take advantage of ephemeral resources, such as twigs, for nests. In long-lived communities (e.g. trees) priority effects may be very important because the tree will maintain its hold on the colonization site for many years (Palmer et al. 2002). For twig-nesting ants, in contrast, nests are relatively short-lived, and ants must be constantly relocating, and establishing new nests. Furthermore, *A. instabilis* are patchily distributed in the environment and the distribution changes with time and with management activities of the farmers (Philpott 2005, Vandermeer et al. 2008, Perfecto et al. pers. comm.). Thus, the spatial and temporal variation in *A. instabilis* patches, and not just effects of this dominant species at one point in time may be responsible for maintaining diversity of the twig-nesters in this community.

Here, I demonstrate that the presence of *A. instabilis*, a dominant ant species, contributes to community assembly of twig-nesting ants by affecting nest-founding processes. Additional studies are necessary for fully understanding the role of this dominant species. In coffee agroecosystems, nest-sites are a limiting resource and thus strong competition for nest sites may exist (Philpott and Foster 2005). Indeed, nest site takeovers have been observed in the study site, and ants readily compete for nest sites when displaced from natural nests (Livingston and Philpott unpubl.). In addition, nest sites are differentially limited in areas with and without a dominant canopy ant. In order to fully explore the effects of *A. instabilis* on twig-nesting ant communities, additional manipulations could be useful. For example, moving *A. instabilis* nests to areas differing in vegetation structure and noting the impacts on naturally-occurring twig-nesting ant richness and composition would help determine whether *A. instabilis* presence or vegetation structure are more important in twig-nesting ant assembly. Additionally, one could add occupied natural or artificial nests to areas with and without *A. instabilis* to see if colonies persist. Such experiments would help separate the effects of dispersal limitation and recruitment with and without the influence of this canopy dominant ant. Although moving *A. instabilis* colonies may prove logistically difficult, transplants of twig-nesting ant colonies are feasible and such work is currently planned.

Acknowledgements – I thank G. Dominguez, B. E. Chilel and G. Lopez Bautista for assistance in placing and harvesting artificial nests and conducting vegetation surveys. K. Ennis, A. De la Mora, R. Friedrich, D. G. Livingston, G. Pardee and J. Vandermeer provided helpful comments on the manuscript. Dr G. Ibarra Nunez provided logistical support. I thank the Peters Foundation and Finca Irlanda for permission to conduct research at their farm. Financial support for this work came from NSF no. 0349388 to I. Perfecto and J. Vandermeer and from the Univ. of Toledo.

References

Albrecht, M. and Gotelli, N. 2001. Spatial and temporal niche partitioning in grassland ants. – Oecologia 126: 134–141.

Andersen, A. N. 2008. Not enough niches: non-equilibrial processes promoting species coexistence in diverse ant communities. – Austral Ecol. 33: 211–220.

Andersen, A. N. and Patel, A. D. 1994. Meat ants as dominant members of Australian ant communities: an experimental test of their influence on the foraging success and forager abundance of other species. – Oecologia 98: 15–24.

Armbrecht, I. et al. 2004. Enigmatic biodiversity correlations: ant diversity responds to diverse resources. – Science 304: 284–286.

Blüthgen, N. et al. 2004. Bottom–up control and co-occurrence in complex communities: honeydew and nectar determine a rainforest ant mosaic. – Oikos 106: 344–358.

Byrne, M. M. 1994. Ecology of twig-dwelling ants in a wet lowland tropical forest. – Biotropica 26: 61–72.

Carvalho, K. S. and Vasconcelos, H. L. 1999. Forest fragmentation in central Amazonia and its effects on litter-dwelling ants. – Biol. Conserv. 91: 151–157.

Cerda, X. et al. 1997. Thermal disruption of transitive hierarchies in Mediterranean ant communities. – J. Anim. Ecol. 66: 363–374.

Chesson, P. L. and Warner, R. R. 1981. Environmental variability promotes coexistence in lottery competitive systems. – Am. Nat. 117: 923–943.

Colwell, R. K. 2005. EstimateS: statistical estimation of species richness and shared species from samples. Ver. 7.5. User's guide and application published at: <http://purl.oclc.org/estimates>.

Dunn, R. R. et al. 2007. Temporal patterns of diversity: assessing the biotic and abiotic controls on ant assemblages. – Biol. J. Linn. Soc. 91: 191–201.

Forsman, J. T. et al. 2001. Effects of predation on community assembly and spatial dispersion of breeding forest birds. – Ecology 82: 232–244.

Frederickson, M. E. 2006. The reproductive phenology of an Amazonian ant species reflects the seasonal availability of its nest sites. – Oecologia 149: 418–427.

Hämmer, Ø. et al. 2001. PAST: paleontological statistics software package for education and data analysis. – Palaeontol. Electronica 4: 9.

Hölldobler, B. and Wilson, E. 1990. The ants. – Harvard Univ. Press.

Holt, R. D. 1984. Spatial heterogeneity, indirect interactions, and the coexistence of prey species. – Am. Nat. 124: 377–406.

Holway, D. et al. 2002. The causes and consequences of ant invasions. – Annu. Rev. Ecol. Syst. 33: 181–233.

Hubbell, S. P. and Foster, R. B. 1986. Commonness and rarity in a neotropical forest: implications for tropical tree conservation. –In: Soule, M. E. (ed.), Conservation biology: the science of scarcity and diversity. Sinauer, pp. 205–231.

Janzen, D. H. 1967. Interaction of the bull's horn acacia (*Acacia cornigera* L.) with an ant inhabitant (*Pseudomyrmex ferruginea* F. Smith) in eastern Mexico. – Univ. of Kansas Sci. Bull. 47: 315–558.

Kaspari, M. and Weiser, M. 2000. Ant activity along moisture gradients in a neotropical forest. – Biotropica 32: 703–711.

Kaspari, M. et al. 2000. Energy, density, and constraints to species richness: ant assemblages along a productivity gradient. – Am. Nat. 155: 280–293.

Kneitel, J. M. and Chase, J. M. 2004. Disturbance, predator, and resource interactions alter container community composition. – Ecology 85: 2088–2093.

Leston, D. 1978. Neotropical ant mosaic. – Ann. Entomol. Soc. Am. 71: 649–653.

Longino, J. T. 2009. Ants of Costa Rica. <http://academic.evergreen.edu/projects/ants/AntsofCostaRica.html>. Accessed Sept. 2009.

McGlynn, T. P. 2006. Ants on the move: resource limitation of a litter-nesting ant community in Costa Rica. – Biotropica 38: 419–427.

Nestel, D. and Dickschen, F. 1990. The foraging kinetics of ground ant communities in different Mexican coffee agroecosystems. – Oecologia 84: 58–63.

Paine, R. T. 1966. Food web complexity and species diversity. – Am. Nat. 1907: 65–75.

Palmer, T. M. et al. 2002. Burning bridges: priority effects and the persistence of a competitively subordinate acacia–ant in Laikipia, Kenya. – Oecologia 133: 372–379.

Palmer, T. M. et al. 2003. Competition and coexistence: exploring mechanisms that restrict and maintain diversity within mutualist guilds. – Am. Nat. 162: 63–79.

Parr, C. L. 2008. Dominant ants can control assemblage species richness in a South African savanna. – J. Anim. Ecol. 77: 1191–1198.

Parr, C. L. and Gibb, H. 2010. Competition and the role of dominant ants. – In: Lach, L. et al. (eds), Ant ecology. Oxford Univ. Press, pp. 77–96.

Perfecto, I. and Vandermeer, J. 1996. Microclimatic changes and the indirect loss of ant diversity in a tropical agroecosystem. – Oecologia 108: 577–582.

Perfecto, I. and Vandermeer, J. 2008. Spatial pattern and ecological process in the coffee agroforestry system. – Ecology 89: 915–920.

Philpott, S. 2005. Effects of shade tree pruning on arboreal ants in coffee agroforestry systems. – Agrofor. Syst. 64: 219–224.

Philpott, S. and Foster, P. 2005. Nest-site limitation in coffee agroecosystems: artificial nests maintain diversity of arboreal ants. – Ecol. Appl. 15: 1478–1485.

Philpott, S. et al. 2006. Effects of management intensity and season on arboreal ant diversity and abundance in coffee agroecosystems. – Biodiv. Conserv. 15: 139–155.

Ribas, C. R. et al. 2003. Tree heterogeneity, resource availability, and larger scale processes regulating arboreal ant species richness. – Austral Ecol. 28: 305–314.

Sanders, N. J. et al. 2003. Community disassembly by an invasive species. – Proc. Natl Acad. Sci. USA 100: 2474–2477.

Sanders, N. et al. 2007. An ant mosaic revisited: dominant ant species disassemble arboreal ant communities by co-occur randomly. – Biotropica 39: 422–427.

Savolainen, R. and Vepsäläinen, K. 1988. A competition hierarchy among boreal ants: impact on resource partitioning and community structure. – Oikos 51: 135–155.

Stanton, M. L. et al. 2002. Competition–colonization trade-offs in a guild of African acacia-ants. – Ecol. Monogr. 72: 347–363.

Torres, J. and Snelling, R. 1997. Biogeography of Puerto Rican ants: a non-equilibrium case? – Biodiv. Conserv. 6: 1103–1121.

Vandermeer, J. et al. 2008. Clusters of ant colonies and robust criticality in a coffee agroecosystem. – Nature 451: 457–459.

Wootton, J. T. 1994. Predicting direct and indirect effects: an integrated approach using experiments and path analysis. – Ecology 75: 151–165.

Yodzis, P. 1978. Competition for space and the structure of ecological communities. – Springer.