A thesis entitled:

Ground-foraging ant diversity and the role of an aggressive ant (*Azteca instabilis*) in coffee

agroecosystems

by

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A thesis submitted

in partial fulfillment of the requirements

for the degree of Master of Science

(Natural Resources and Environment)

in the University of Michigan

December 16, 2010

Thesis Committee:

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ABSTRACT

Conventional ecological theory on competition and competitive exclusion states that competition should limit diversity. However, diversity of all species is more common than competitive exclusion would suggest, especially in the tropics. Ants are a great study organism to ask questions of diversity and competition due to their high diversity and their relatively sessile nature of their nest. Similarly, agroecosystems offer a good habitat to study patterns of diversity due to the relative homogeneity of the habitat within each management regime. We studied the patterns of alpha diversity (local species richness) of ants from two different assemblages (coffee-foraging and ground-foraging) in the presence of a dominant and territorial ant species (*Azteca instabilis*) in a coffee agroecosystem. We hypothesized the that alpha diversity will be the highest at intermediate distance from the *A. instabilis* nests because close to the nests, the aggressive *Azteca* ants are successful at excluding other species, but far away form *A. instabilis* the normal competitive exclusion operates and reduces diversity to one or just a few species. We surveyed eight sites across three management intensities (high, moderate and low shade) for coffee-foraging ants (2 of 8 sites) and ground-foraging ants (all sites) and examined the species richness of each assemblage against the distance from the *A. instabilis* nest. We found no significant relationship between species richness and distance from *A. instabilis* for the coffee-foraging ant species. However, there was a consistent negative trend across high and moderate shade. This relationship was significant in five of six sites in the high and moderate shade plots. Species richness declines with increasing distance from the dominant ant (*A. instabilis*). In the low shade, the relationship was reversed in one site (positive trend) and nonexistent in the other. While correlative, this data suggests that competition may be shaping

the assemblage patterns found. Furthermore the interactions between *A. instabilis* and other ground-foraging ants may actually increase ant species richness.

TABLE OF CONTENTS

INTRODUCTION

Explaining patterns of diversity is a common theme in ecology. The ideas and theories used to explain these patterns either attempt to identify what the potential species composition could be, or they attempt to explain how and why diversity is maintained. Some ideas emphasize the regional processes of species formation, dispersal, immigration and emigration (Ricklefs 1987; Liebold et al. 2004; Volkov et al. 2003; Loreau and Mouquet 1999). These processes are effective at predicting potential species assemblages or *what* assemblages may be observed in particular habitats, but it does not answer *how* diversity is maintained at the local scale through the coexistence of species.

Among the more popular ideas explaining patterns and maintenance of local diversity and coexistence are habitat complexity, disturbance, predation and competition. Habitat complexity may facilitate the use of resources and prevent competitive exclusion (Sarty et al. 2006). Habitat diversity itself seems to promote higher ant diversity (Armbrect et al. 2004; Philpott and Foster 2005). Furthermore, habitat complexity offers more refugia from which to escape predation and increase species richness (Caley and John 1996).

Intermediate disturbances are thought to maintain diversity and coexistence by creating sufficient instability in the environment so as to prevent the exclusion of inferior competitors (Connell 1978). Disturbance also maintains habitat complexity (resource and structural complexity) increasing the likelihood of finding an area suitable for a larger number of species.

Predation is another interaction used to explain the maintenance of diversity via coexistence. In this case, predators interfere with the competitive interactions between prey species reducing exclusion of inferior competitors and increasing the number of species. For example, ant parasitoids can act to impede the competitive success of dominant ant species

against inferior ant competitors (Philpott 2005). Paine's (1966) classic study on intertidal communities revealed that the presence of a predator increases overall species richness of the local community. Paine's (1966) study was the first to demonstrate the influence of predation on competitive interactions but it also lead to the idea that one species in a community may have a disproportional effect on it's community relative to its abundance. These species are termed 'keystone species.'

Competition is thought to limit coexistence between species that consume similar resources (Lotka 1925; Volterra 1926; Gause 1934; MacArthur and Levins 1964). While competition negatively effects all organisms involved, the burden of the negative interaction is rarely equally displaced between individuals. The unequal distribution of the negative interaction can result in a competitive hierarchy where dominant competitors outcompete inferior competitors and lower species richness. However, some other models of competitive interactions demonstrate that there are several ways that interspecific competition can lead to coexistence. Trade-offs in competitive ability can lead to greater coexistence between competing species (Goldberg and Landa 1991, Fellers 1987). Additionally two species may coexist on a shared resource if the more efficient consumer has a more non-linear functional response that generates consumer resource cycles (Armstrong and McGeHee 1980; Vandermeer 2002).

Ants offer a unique way to study patterns in diversity and co-existence because they represent a diverse family of insects (Formicidae). Competition is the focus of ant ecology and has long been held as the major determinant in structuring ant communities (Levinsg and Trianello 1981;Levings and Frank 1982). For one, the spatio-temporal longevity of an ant nest increases the likelihood of competition for space. Ants nests found in the soil and tree cavities are relatively long-lived and sessile; only moving to new sites if highly disturbed. As a result one

ant colony may reside in the same location for many years (Holldobler and Wilson 1990). Furthermore, many ant species require and consume similar resources. These life history traits among guilds of ants have lead to the assumption that many ant species are competing for both limited nesting sites and shared food resources.

Ant mosaics provide additional support to the idea that interspecific competition shapes ant communities. Several studies show that dominant ant species can form patchy spatial distributions in which the strongest competitors will have habitats that do not overlap, creating a mosaic-like pattern in local habitats (Majer 1972; Room 1971). In ant mosaics, interspecific competition is believed to lead to competitive exclusion of the least competitive species and limit local species richness, however in areas without strong competitors weaker competitors can coexist. Canopy ant communities are the focus of much of the ant mosaic research, but there is some evidence that ant mosaics may occur with ground-foraging ants as well (Figure 1).

If ant-mosaics (and therefore also competitive exclusion) are common in ant assemblages, we ask: how ant richness is maintained in habitats with strong ant competitors? While Parr (2008) suggests that dominant ant species may control species richness of an ant assemblage, the study is unable to attribute the effect found to one species within the community. Applying the idea of a keystone species to the likely competitive interactions between ant species may explain increased richness in ant communities. In this case a keystone ant species of one assemblage may reduce the effects of competition between ants of another assemblage through indirect competition (rather than through predation) with the superior ant competitors of the alternate guild. Here, we examine the species richness of two ant guilds, the coffee-foraging ants and the ground foraging ants in relation to the aggressive dominant arboreal ant, *Azteca instabilis*.

The habitat of a coffee agroecosystem is relatively homogenous compared to tropical humid forests due to the prevalence of the crop species and the planted shade trees. *A. instabilis* is a dominant canopy ant found throughout the neotropics in coffee agroecosystems (Vandermeer et al. 2008). It forms large carton nests in trees and has a well-documented mutualism with the hemipteran coffee pest, the green scale insect, *Coccus viridus* (Perfecto and Vandermeer 2006). *Azteca* is further associated with many organisms (parasitoids, fungi, beetles and ants) in coffee systems and is thought to act as a keystone species in this habitat (Figure 2; Vandermeer et al. 2010). The purpose of this study is to determine if *Azteca instabilis* could be acting as a keystone species to the ground-foraging ant assemblage in the neotropical coffee agroecosystem.

METHODS

Study Site

The study was completed in two adjacent coffee farms in the Soconusco region of Chiapas, Mexico 40 km NE of Tapachula (15° 11' N, 92° 20' W). Finca Irlanda is a 280-hectare shaded organic coffee farm with a uniform distribution of shade trees that represent 215 shade tree species (Vandermeer et al. 2008) and encompasses two management styles referred to in this study as high and moderate shade coffee production. Within the active production area, shade cover is moderate with between 50-70% shade (moderate shade). In the moderate shade area we have established a 45-hectare plot with approximately 9,000 shade trees mapped and surveyed for presence of *A. instabilis* for the past 6 years (Figure 3; Perfecto and Vandermeer 2008). The high shade area of Finca Irlanda produces coffee, but is virtually unmanaged and has approximately 70% canopy cover (high shade). In the high shade area we have established another 6-hectare plot using the same methods for tree marking, location and hosting *A. instabilis*

4

data. Finca Hamburgo is a large (1000 ha.) coffee farm that has much lower shade cover (15-30%), much lower shade tree diversity and employs the use of more conventional management techniques including the application of pesticides and herbicides (low shade). While there is no established plot in Hamburgo we have located all nests of *A. instabilis* in a 10 ha. region of the farm. According to the standard classification system of Moguel and Toledo (1999), the high shade area is consistent with the description of a traditional polyculture, the moderate shade area is a commercial polyculture, and low shade is consistent with a shaded monoculture.

Ant sampling

Ant surveys took place in June and July 2009 in the morning hours between 7:00-11:00am at each of the three shaded coffee production areas (low, moderate and high shade) within eight plots. In the high shade we established two plots (plot M: 24m x 20m; site N: 20m x 20m), in the moderate shade we established four plots (plot F: 48m x 48m; plot Q: 40m x 40m; plot V: 32m x 24m; plot B: 24m x 24m) and in the low shade we established two plots (plot P: 24m x 24m; plot R: 24m x 24m). Each plot was established around a cluster of *A. instabilis* nests residing in shade trees above the coffee bushes. The number of nests in each plot varied from 2-8 (Table 1). For all plots we established a grid with a sampling point at every 4m or every 2m across the entire area of the plot.

Coffee bush sampling

We baited for coffee-foraging ants at only the two largest plots within the moderate shade (plots F and Q). For both sites we baited with tuna in oil at each coffee bush closest to every 4m point established for the ground-foraging ants. Tuna in oil is a commonly used to bait ants and is estimated to attract nearly 30% of the ants present. On each bush we had two baits: one at the lowest branch and one close to the top branch. After placing one teaspoon of tuna on both the

low and high branches we waited 20 minutes and recorded each species found within 10 cm of the bait. For ants we could not identify to species or morphospecies in the field we collected a sample placed in 75% ethyl alcohol and brought them back to the lab for identification.

Ground sampling

We baited for ground ants at all 8 sites using tuna in oil. At the two largest sites we placed one teaspoon of tuna on the ground at every 4 m forming a grid pattern, and at each of the remaining smaller sites we placed one teaspoon of tuna on the ground every 2 m. We waited 20 minutes and recorded each species found within 10 cm of the bait. For species we could not identify to species or morphospecies in the field we collected a sample and brought them back to the lab for identification.

Analysis

Estimated richness of species was calculated for each lattice point within each plot. We summed the observed number of unique species at the bait and the 8 nearest neighbor points (the Moore neighborhood). This was done to quantify those species that were in the area but were not observed near the baits. We eliminated those baits on the edges because the estimated richness of those points could only be informed by 5 neighbor points for the edges and 3 neighbor points for the corners. We then regressed the estimated richness of ground-foraging ant species against the distance to the nearest nest of *A. instabilis* and chose the best regression model with ANOVA test linear models with quadratic model fit comparing the sum-of-squares of the two models. Estimated richness was calculated using MatLab and regression analysis and model fitting was done with StatPlus.

RESULTS

Coffee bush sampling

There were differing results for the two plots in which we baited for ants on coffee plants, both in moderate shade. In Site F we found no significant relationship between estimated richness and distance to the nearest *A. instabilis* nest (Figure 4a, 4c; R^2=0.007, *P*=0.375). However, in Site Q we found a significant negative relationship (Figure 4b, 4d; R^2=0.154, *P*=0.006).

Ground sampling

In both high shade plots (Plot M, Plot N) we found a significant relationship between estimated species richness of ground-foraging ants and the distance to the nearest nest of *A. instabilis* (Figure 5; Plot M: R^2=0.196, *P*<0.0001, Plot N: R^2=0.288, *P*<0.0001). This relationship was found to be significantly stronger using a negative quadratic model rather than a negative linear model (Plot M: $F_{97,96}$ = 23.33, *P* <0.0001; Plot N: $F_{79,78}$=13.41, *P* <0.0001).

In the moderate shade pots F, V and B we found significant negative relationships between estimated species richness and distance to the nearest *A. instabilis* nest (Figure 6a, 6c, 7c, 7d; Plot F: R^2=0.290, *P* <0.0001; Plot V: R^2= 0.134, *P* =0.00001; Plot B: R^2=0.049, *P* =0.015). Plot Q did follow the same negative trend as the other plots with moderate shade but the trend was not significant (Figure 6b, 6d; Plot Q: R^2=0.039, *P* =0.208). All plots in the moderate shade, except for Plot B, showed significant improvement in the relationship with a negative quadratic equation (Plot F: $F_{119,118}$ =38.91, *P* < 0.0001; Plot Q: $F_{79,78}$=2.52, *P* <0.0001; Plot V: $F_{163,162}$=22.58, *P* <0.0001; Plot B: $F_{119,118}$=1.08, *P* =0.330).

In the low shade Plot P, there was no significant relationship found between estimated species richness and distance to the nearest *A. instabilis* nest (Figure 8b, 8d; Plot P: R^2= 0.023, *P*

=0.098) and did not benefitted significantly from using a quadratic model to fit the data (Plot P: F=1.19, P =0.178). However in Plot R there was a significant *positive* relationship found in estimated species richness and increasing distance from *A. instabilis* (Figure 8a, 8c; Plot R: R^2=0.222, P <0.0001). Neither plot in the low shade benefitted significantly from using a quadratic model (Site R: $F_{119,118}$=10.02, P <0.0001).

We averaged the R^2 value for each plot with a negative trend between species richness and distance from *A. instabilis* in each shade category and performed an ANOVA comparing the average correlations. For the only plot with a positive correlation (Plot R), we used an R^2 of 0.00 to signify that there was no negative correlation for that plot. The results did not show significant differences between the three shade levels and the R^2 value (Figure 9; $F_{2,5}$=9.45, P =0.14), however, there is a declining trend, where shade cover declines the R^2 value also declines.

DISCUSSION

Studies in ant ecology have long sought to determine what mechanisms structure ant communities. The findings here demonstrate that the aggressive, dominant ant, *A. instabilis* influences species richness of the the arboreal and ground-foraging ant community in coffee agroecosystems. Although this relationship is complicated and varies with shade cover and ant guild (arboreal and ground foraging ants), there seems to be a general trend pattern of a halo effect. That is, *A. instabilis* appears to have a negative effect on species richness very close to their nest but a positive effect at a distance between 5 to 10 meters, then, at higher distances, species richness declines again (Figures 5, 6, and 7). The obvious exception to this pattern was for the two plots in the low shade sites where the relationship between species richness and distance from *A. instabilis* nests is non-existent (Figure 8d) or positive (Figure 8c). Another

exception to this pattern was found for the arboreal ants, since a negative linear relationship explained more variance than a quadratic model (Figure 4), and one of the plots in the moderate shade sites (Plot Q) for the ground foraging ants, where the best fit was also a negative linear relationship (Figure 7d).

Our results are consistent with previous studies that show dominant ant species can structure local ant communities. In twig-nesting ant assemblages, *A. instabilis* affects the most common twig-nesting species, but did not affect more rare species (Philpott 2010). In ground-foraging assemblages Gibb (2004) found that the exclusion of a single dominant species increases the dominance of other ecologically similar species, but did not show increases in species richness. Parr (2008) showed that a moderate abundance of multiple dominant ant species yields higher species richness. In both cases of ground-foraging ant species, however, the studies examine only dominant ant species within a single ant assemblage and the dominant ant(s) were numerically dominant, rather than exclusively behaviorally dominant as with *A. instabilis*. For example in Gibb (2004) the dominant ant, *Iridomyrmex purpureus* makes up between 68-84% of all ants present, while in Parr (2008) the five dominant ant species make up a combined 54.5-72.2% of all ants present. In contrast, *A. instabilis* is found on fewer than 4% of all baits (Figure 11) and often makes up > 2% of all species present. Furthermore, these studies did not use spatial explicit data to examine the relationships between dominant and non-dominant species. This study is the first to show that one behaviorally dominant species of a canopy assemblage may be a major factor in spatial structure of ground-foraging ant communities.

Coffee bush ants

The surveys on coffee-foraging ants in the two sites (both within the moderate shade) yielded mixed results; Plot Q had a significant decline in species richness in relation to the location of *Azteca* and in Plot F, while it did yield a decline in species richness, the relationship was not significant. However, in neither case was a non-linear relationship observed. It is possible that our sampling scheme did not include enough coffee bushes very close to the *A. instabilis* nests. Recall that samples in these two plots were taken from plants that were close to the baits place at 4 m distance from each other. Given that the area of strong influence of *Azteca* seems to be just two to three meters, it is possible that our sampling did not included some of the coffee bushes that have the highest *Azteca* activity. It is also possible that the baits attracted ants that are only opportunistic foragers on coffee and therefore are not in direct competition with *A. instabilis*. Due to several studies that document the competitive interactions between *A. instabilis* and other coffee foraging ants (Philpott 2005; Philpott and Foster 2005; Philpott 2010), we think that competition for nesting sites and resources are responsible for the for the trends observed between species richness of coffee-foraging ants and the distance from *A. instabilis*. *A. instabilis* has been shown to strongly affect the most common twig-nesting species and to weakly affect more rare species (Philpott 2010). If this effect applied to coffee-foraging ants, as many of the species in those assemblages overlap, then the relationship observed in this study may be seen caused by competition between stronger and weaker competitors of the coffee-foraging assemblage. In this case weaker species are unaffected by *A. instabilis* and are found closer to *A. instabilis*. Stronger competitors, of which there are fewer, are negatively affected by *A. instabilis* and are only found further from their nests.

Interestingly, the plot that shows no significant relationship for the arboreal ants (Figure 4c) shows a very strong non-linear relationship for the grounds foraging ants (Figure 6c) and the plot that shows a strong relationship with for the arboreal ants (Figure 4d) shows no significant relationship for the ground ants (Figure 6d). This suggest that the lack of an effect for the coffee-foraging ants could be due to a strong ground foraging activity of the ants in that plot. And likewise, that the strong effect observed for the coffee-foraging ants could be due to strong arboreal foraging of *A. instabilis* within that plot. Unfortunately, we don't have data on *Azteca* activity within individual coffee bushes, nor do we have more replicates of plots where both ground and arboreal ants were sampled.

Ground-foraging ants: high and moderate shade

The trend across all 6 sites in both high and moderate shade revealed a negative relationship between ground-foraging ant species richness and distance from *A. instabilis*. All but one of the sites displayed a negative nonlinear relationship (Plot B) and all but one site (Plot Q) were significant. We speculate that the trend is caused by indirect competitive interactions between ants. The most dominant ground-foraging ants in each site tend to form large patches, but these large patches of dominant species rarely overlap (Figure 1). Other species are found within a patch of a dominant species, but they do not tend to form the large patches that are formed by the dominant species. The non-linear negative relationship most likely arise from the strong effect of *A. instabilis* close to its nest. Nearest to the arboreal nest individual ants are constantly traversing across the ground to tend the green scale insects on the coffee plants that are closest to their nest. Since nearest to the nests we see lower richness, we interpret this to be due to the territorial and aggressive behavior of *A. instabilis*. At intermediate distances from the nest (approximately 5 to 10 meters) the influence of the *Azteca* ants is still there, but less intense.

The presence and activity of *A. instabilis* at these intermediate distances lowers the likelihood of occupation of a dominant ground-foraging species, providing other ground-foraging species a greater opportunity for foraging and nesting sites within the peripheral area, just outside the strong influence of *A. instabilis,* creating a diversity halo effect (Figure 10a, 10b). While the interaction between these ground-foraging ant species and *A. instabilis* remains unclear, the trend is consistent and provides some support for the idea that these local interactions are based on competition.

In Plot B the best model was a negative linear model. This may be explained by the comparatively low presence of *A. instabilis* found on baits at this particular site as compared to the others in the moderate shade (Figure 11). Because *A. instabilis* is found less at the baits it is less likely to have a negative influence on the immediate area surrounding the nest and therefore less likely to result in a nonlinear relationship.

The one site that did not show a significant relationship between richness and distance to *A. instabilis* did still show a similar non-linear trend. As part of the management of the coffee farm, during this year there was a farm-wide cut of many of the shade trees. This site experienced some of the heaviest cutting. This particular site had among the highest *A. instabilis* nest density of all the sites (Table 1; Figure 6b) and highest proportion of new shade trees (those trees that are about 10cm dbh). The proportion of nests may affect how discernable the pattern is that we have observed in the other sites. The proportion of shade trees is an indication of how affected the site was to a shade tree cut that occurred the year prior to the survey. Furthermore, two of the most active nests were chopped. While this did not kill the colony it did appear to affect the foraging extent and pattern of *A. instabilis* (personal observation) and create smaller

satellite nests. The creation of these smaller satellite nests is reflected in high nest density for this site.

Ground-foraging ants: low shade

The low shade sites did not display the same trend of declining species richness with distance from *A. instabilis*. In fact, we saw the opposite trend: species richness increased with distance from *A. instabilis*. This may be due to the high activity level of those particular nests both foraging on the ground and in the nests (Table 2). Because the *Azteca* ants in these two plots were very active, we suspect that the same nonlinear relationship may have been visible if the site had been expanded. It is possible that some of the management practices in the low shade sites could be causing a different behavior of the *Azteca* ants. In addition to a lower density and diversity of shade trees, these sites are applied with insecticides, fungicides and herbicides. However, we do not know how these may affect ant behavior. Previous studies have found that the use of insecticides often reduces the diversity of non-target species, including ants (Cattaneo et al. 2006). A reduction in diversity may change the nature of any associations between ant species. Other studies have shown that in low shade habitats, interactions play a minor role in regulating ground-foraging ant communities because higher temperatures interfere with the competitive interactions allowing more heat tolerant species that may be lesser competitors to coexist. (Retana and Cerda 2000; Cerda et al. 1997).

Trends across shade cover

Those sites with the highest negative correlations were in the high shade and those with lowest negative correlations were in the low shade plots. Although the finding was not significant, the trend is clear and would likely get stronger with increased replication within each shade cover category. The mean of the R^2 value in each of the shade cover categories reveals

how the relationship between *A. instabilis* and the other coffee and ground-foraging ant may be affected by shade cover, or by additional unknown management practices. This trend is consistent with previous findings that land use intensification can affect associations between species. Environmental changes, including land use intensification, have been shown to alter species interactions (Tylianakis et al. 2008; Fagan et al. 1999) and other ant community studies that show increased intensification in agroecosytems results in fewer associations between species and fewer species involved in associations (Armbrecht et al. 2005).

Table 1. Plot dimensions, number of *A. instabilis* nests, shade tree density (number of shade trees/plot area), proportion of small shade trees (shade trees of approximately 10 cm dbh), and mean percent shade cover.

Farm	Shade	Site	Size of plot (m)	*A. instabilis* nests	Shade tree density	Nest density	Proportion of shade trees ~ 10 cm (dbh)	Mean % Shade cover
Irlanda	High	M	24 x 20	2	2.9×10^{-2}	4.2×10^{-3}	0	95.39
Irlanda	High	N	20 x 20	2	2.7×10^{-2}	5.0×10^{-3}	0	91.34
Irlanda	Moderate	F	48 x 48	5	1.9×10^{-2}	2.1×10^{-3}	0.065	71.04
Irlanda	Moderate	Q	40 x 40	8	2.2×10^{-2}	5.0×10^{-3}	0.354	57.08
Irlanda	Moderate	V	32 x 24	3	1.6×10^{-2}	3.3×10^{-3}	0.154	78.37
Irlanda	Moderate	B	24 x 24	2	2.0×10^{-2}	3.4×10^{-3}	0	N/A
Hamburgo	Low	R	24 x 24	2	1.9×10^{-2}	3.4×10^{-3}	0	N/A
Hamburgo	Low	P	24 x 24	4	0.5×10^{-2}	6.9×10^{-3}	0	N/A

Table 2. Plot comparisons of the mean activity level of *A. instablis* nests within each plot (measured as the average number of individuals crossing a specified part of the tree in one minute), and the number of occupied baits by *A. instabilis* in ground-foraging surveys done ≤ 2m from each nest.

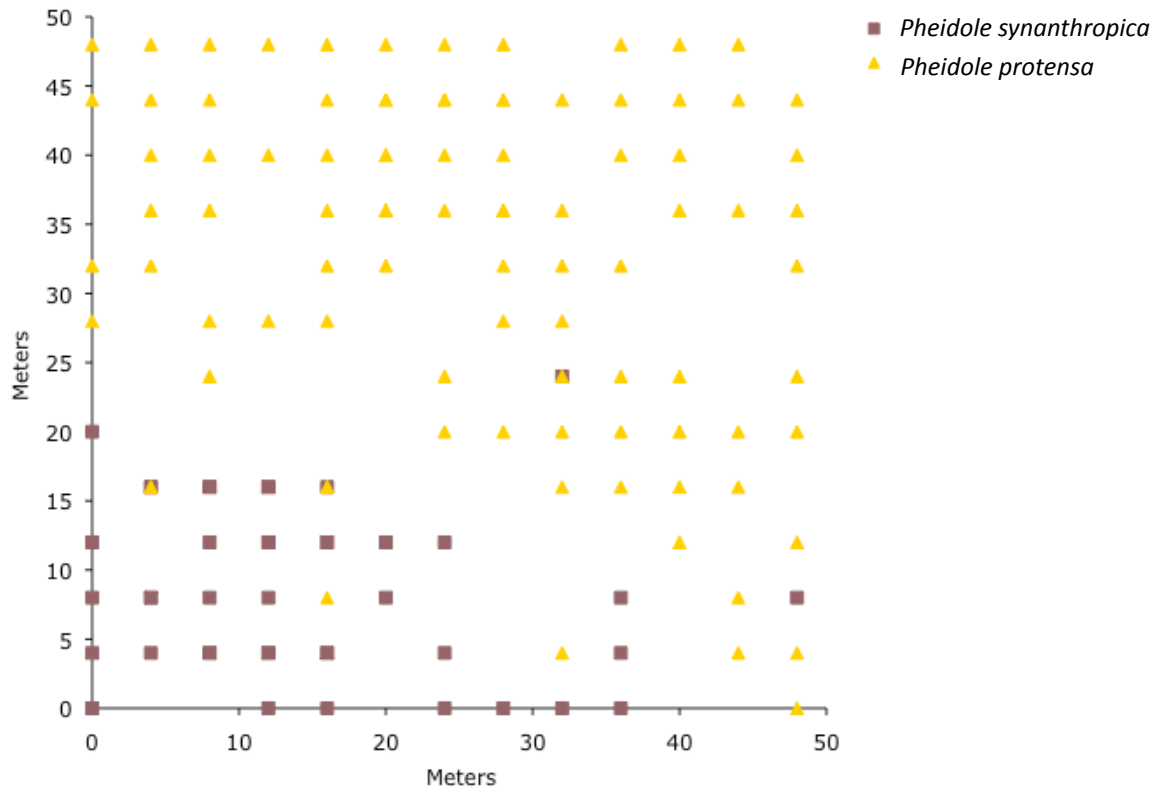| Farm	Shade	Site	Mean activity level of *A. instabilis* nests (ants/min)	Ground-foraging near nests: % occupied baits by *A. instabilis* ≤2m from nest
Irlanda	High	M	22.3	35.0
Irlanda	High	N	N/A	20.0
Irlanda	Moderate	F	76.0	50.8
Irlanda	Moderate	Q	101.5	56.2
Irlanda	Moderate	V	34.1	58.3
Irlanda	Moderate	B	11.8	27.5
Hamburgo	Low	R	244.0	90.0
Hamburgo	Low	P	78.8	32.5

Figure 1. Supportive evidence of ant mosaic in ground-foraging ant assemblages. The presence of two dominant ant species (*Pheidole* ssp) is marked as either a yellow triangle (*Pheidole protensa*) or by a brown square (*Pheidole synanthropica*). The territories of each species is clear (they rarely overlap) and suggestive of an ant mosaic generated by interspecific competition.
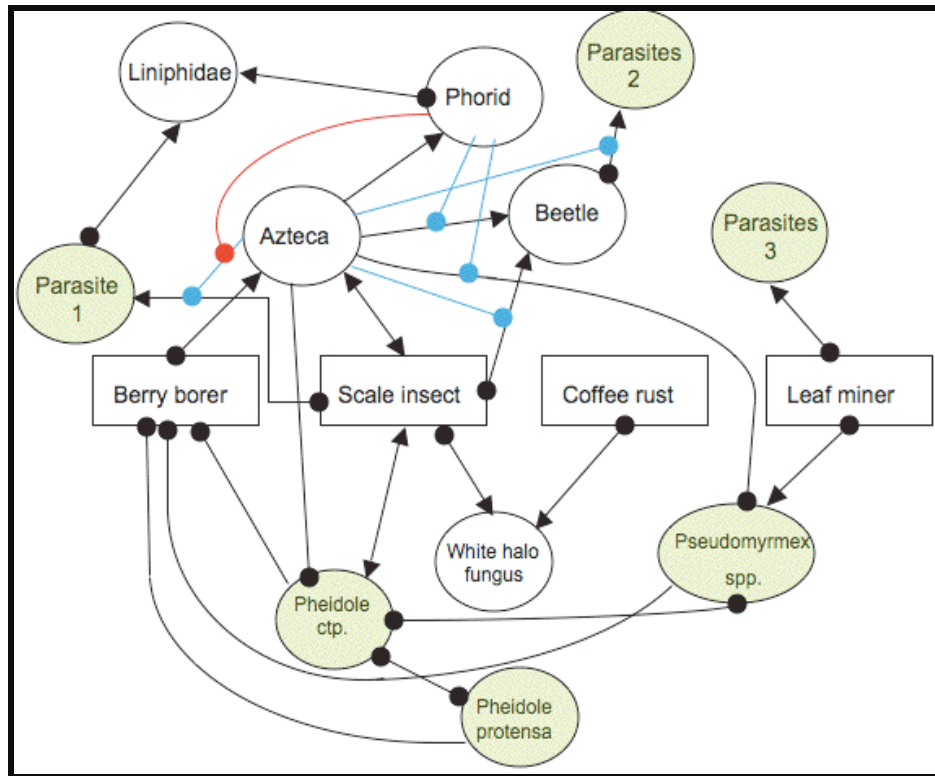
Figure 2. A diagram of the interactions of *A. instabilis* with several other species and groups of species studied over the last 10 years in the coffee agroecosystem in Finca Irlanda, Chiapas, Mexico. Positive effects are symbolized with an arrow, negative effects are symbolized with a circle. Indirect effects are in blue and trait-mediated indirect effects are in red (from Vandermeer et al., 2010).
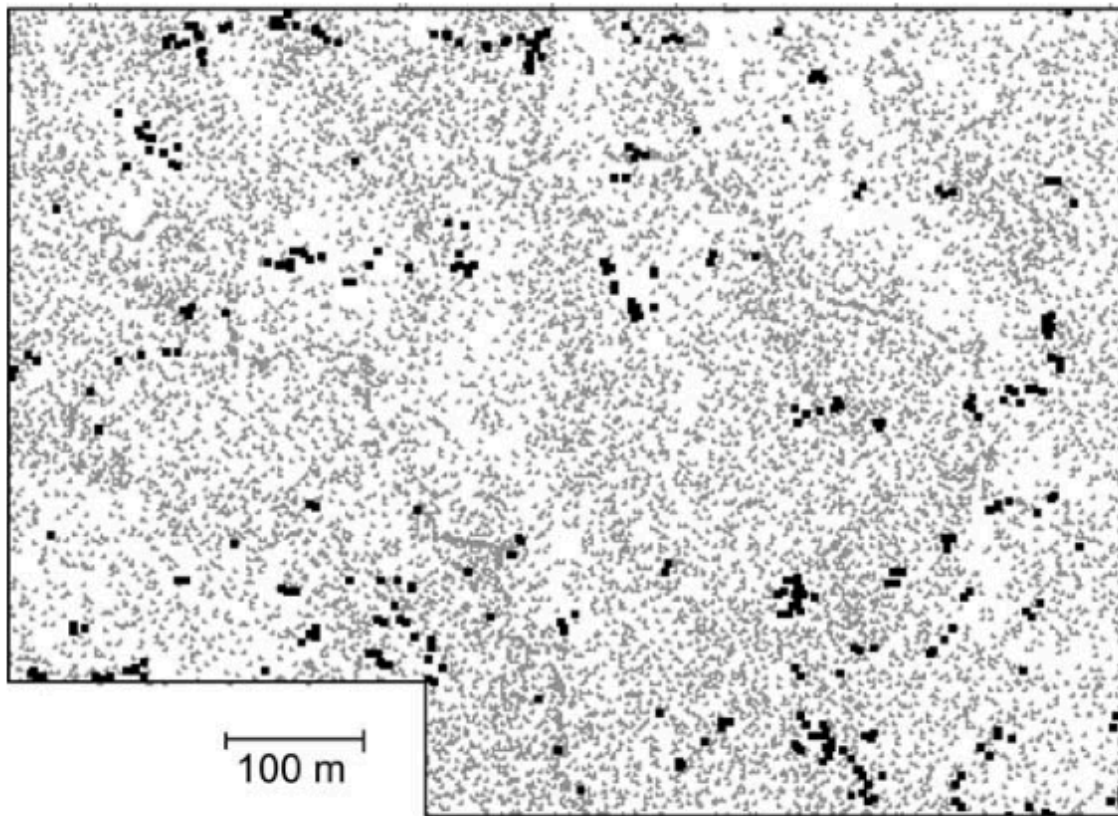
Figure 3. A map of the 45-ha. plot established in Finca Irlanda, a shaded coffee agroecosystem. Gray dots represent shade trees. Black dots represent shade trees occupied by *A. instabilis* (from Perfecto and Vandermeer 2008).
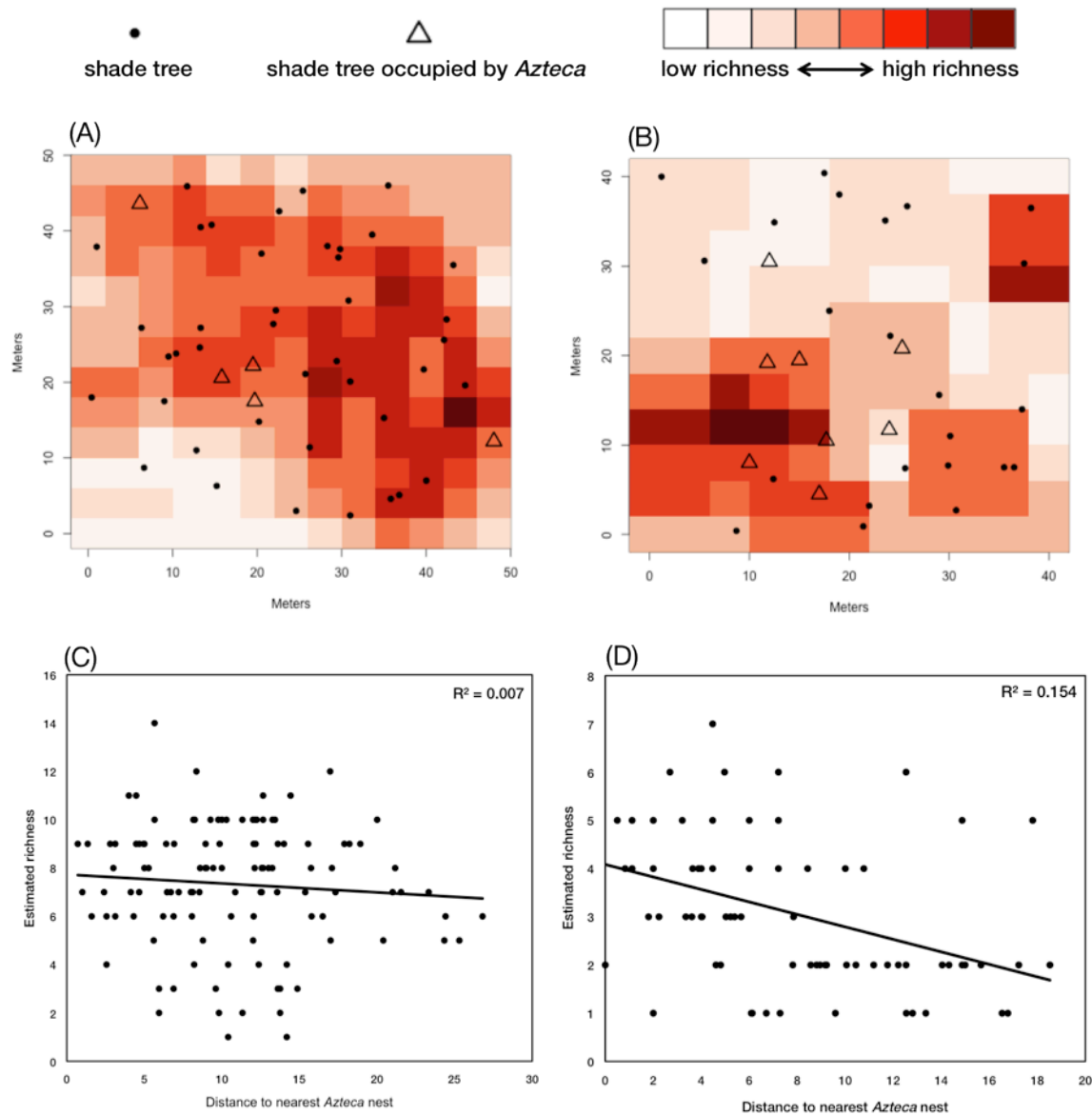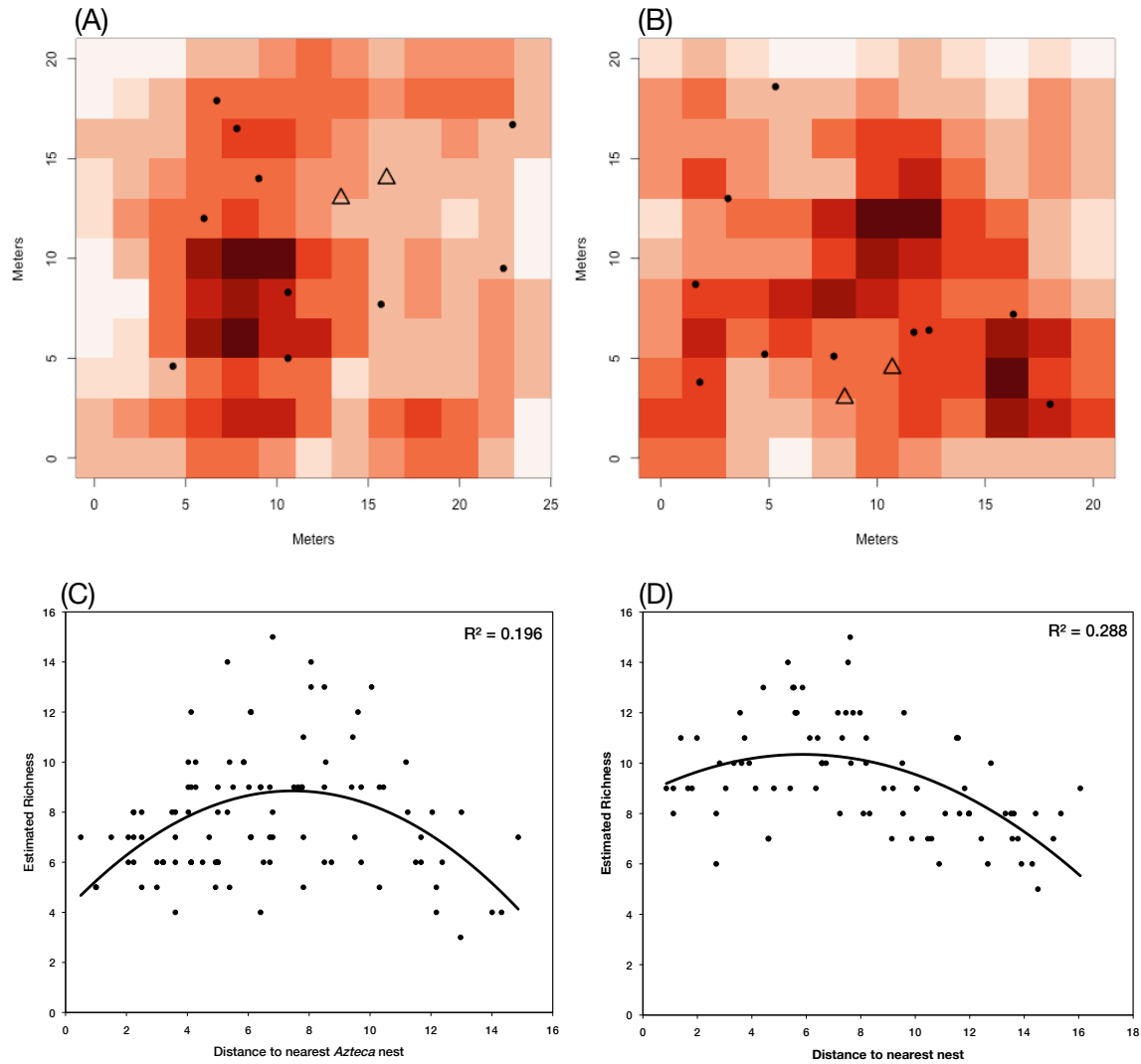
Figure 4. (A)-(B) Spatially explicit representations of results from coffee-foraging ant surveys in (A) Plot F and (B) Plot Q. Each sampling point (every 4m) is represented by a red colored square with the shade of the square indicating the number of ant morphospecies present. Darker red indicates a higher number of morphospecies present. Small black dots represent shade trees in the plot. Small black triangles represent shade trees occupied by *Azteca instabilis*. (C)-(D) Regressions of the results above (A. R^2=0.007, P=0.375; B. R^2=0.154, P=0.006). Each point represents a sampling point within (C) Plot F, (D) Plot Q.

Figure 5. (A)-(B) Spatially explicit representations of results from ground-foraging ant surveys in high shade plots: (A) Plot M and (B) Plot N. Each sampling point (every 2m) is represented by a red colored square with the shade of the square indicating the number of ground-foraging ant morphospecies present. Darker red indicates a higher number of morphospecies present. Small black dots represent shade trees in the plot. Small black triangles represent shade trees occupied by *Azteca instabilis*. (C)-(D) Regressions of the results above (A. R^2=0.196, P<0.0001; B. R^2=0.288, P<0.0001). The number of ground-foraging ant species declines with increasing distance from the nearest *Azteca* nest. Each point represents a sampling point within (C) Plot M or (D) Plot N.
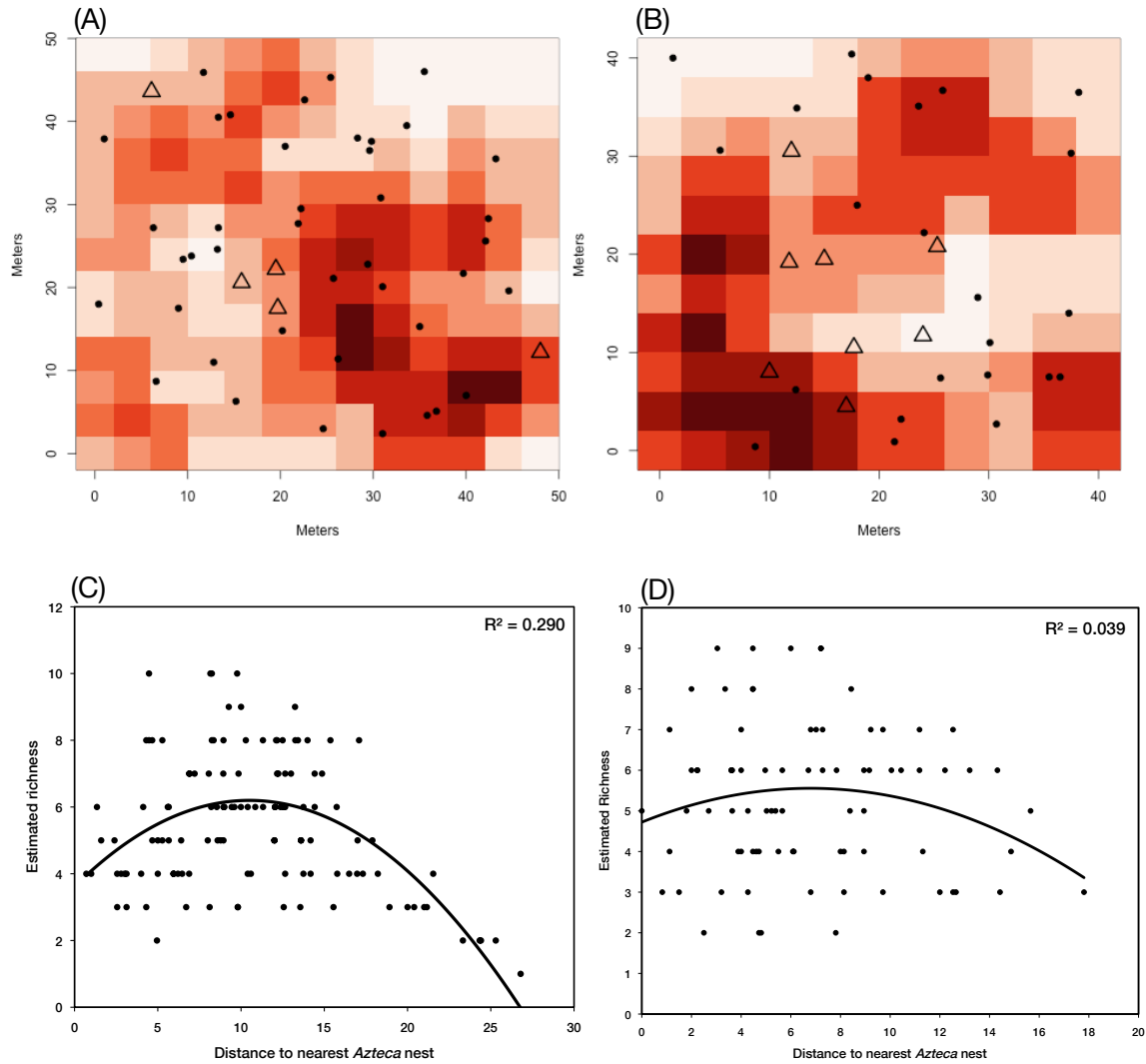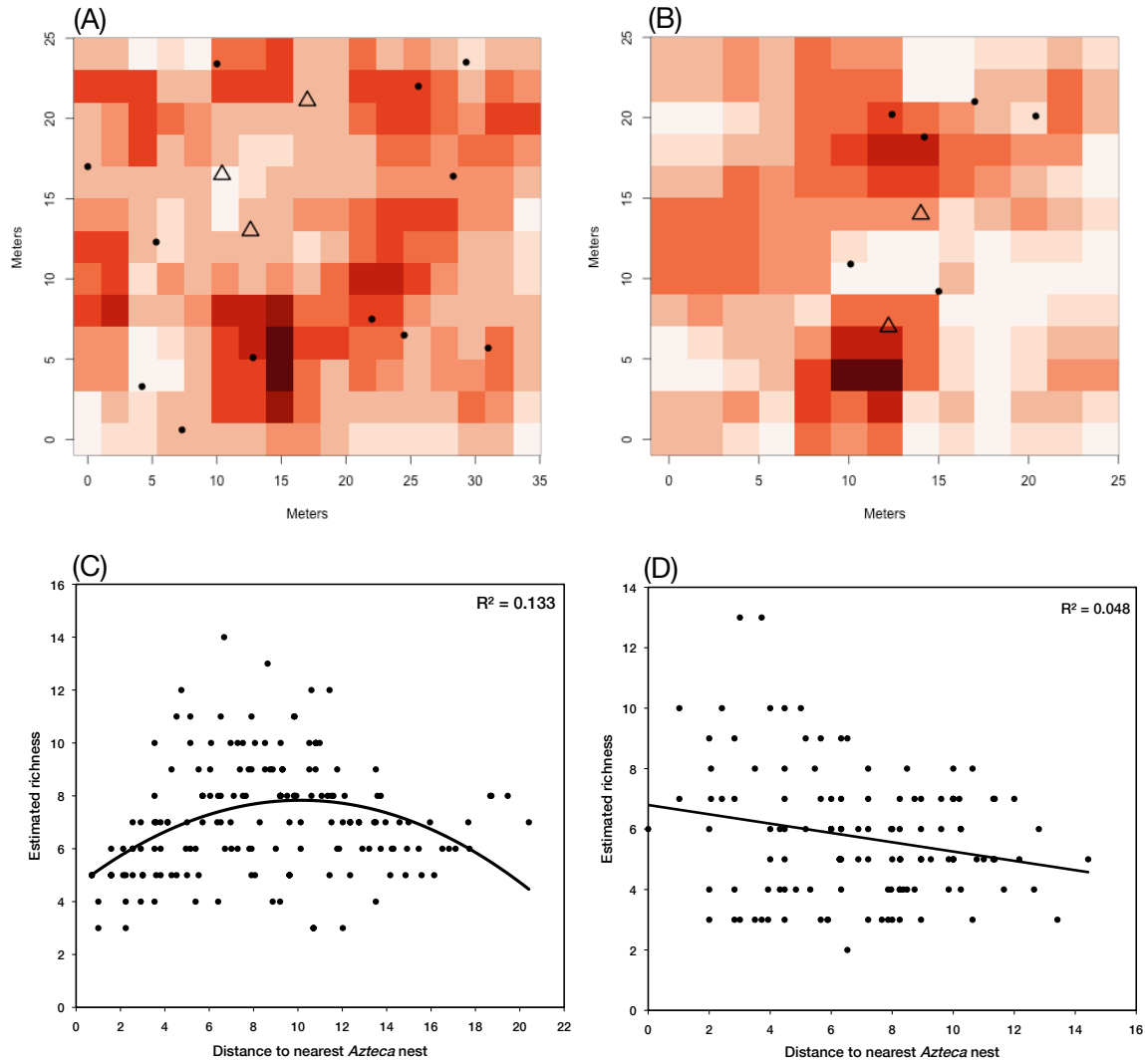
Figure 6. (A)-(B) Spatially explicit representations of results from ground-foraging ant surveys in moderate shade plots: (A) Plot F and (B) Plot Q. Each sampling point (every 4m) is represented by a red colored square with the shade of the square indicating the number of ground-foraging ant morphospecies present. Darker red indicates a higher number of morphospecies present. Small black dots represent shade trees in the plot. Small black triangles represent shade trees occupied by *Azteca instabilis*. (C)-(D) Regressions of the results above (A. R^2=0.290, *P* <0.0001; B. R^2=0.039, *P* =0.208). The number of ground-foraging ant species declines with increasing distance from the nearest *Azteca* nest. Each point represents a sampling point within (C) Plot F, (D) Plot Q.

Figure 7. (A)-(B) Spatially explicit representations of results from ground-foraging ant surveys in moderate shade plots: (A) Plot V and (B) Plot B. Each sampling point (every 2m) is represented by a red colored square with the shade of the square indicating the number of ground-foraging ant morphospecies present. Darker red indicates a higher number of morphospecies present. Small black dots represent shade trees in the plot. Small black triangles represent shade trees occupied by *Azteca instabilis*. (C)-(D) Regressions of the results above (A. R^2= 0.134, P =0.00001; B. R^2=0.049, P =0.015). The number of ground-foraging ant species declines with increasing distance from the nearest *Azteca* nest. Each point represents a sampling point within (C) Plot B, (D) Plot B.
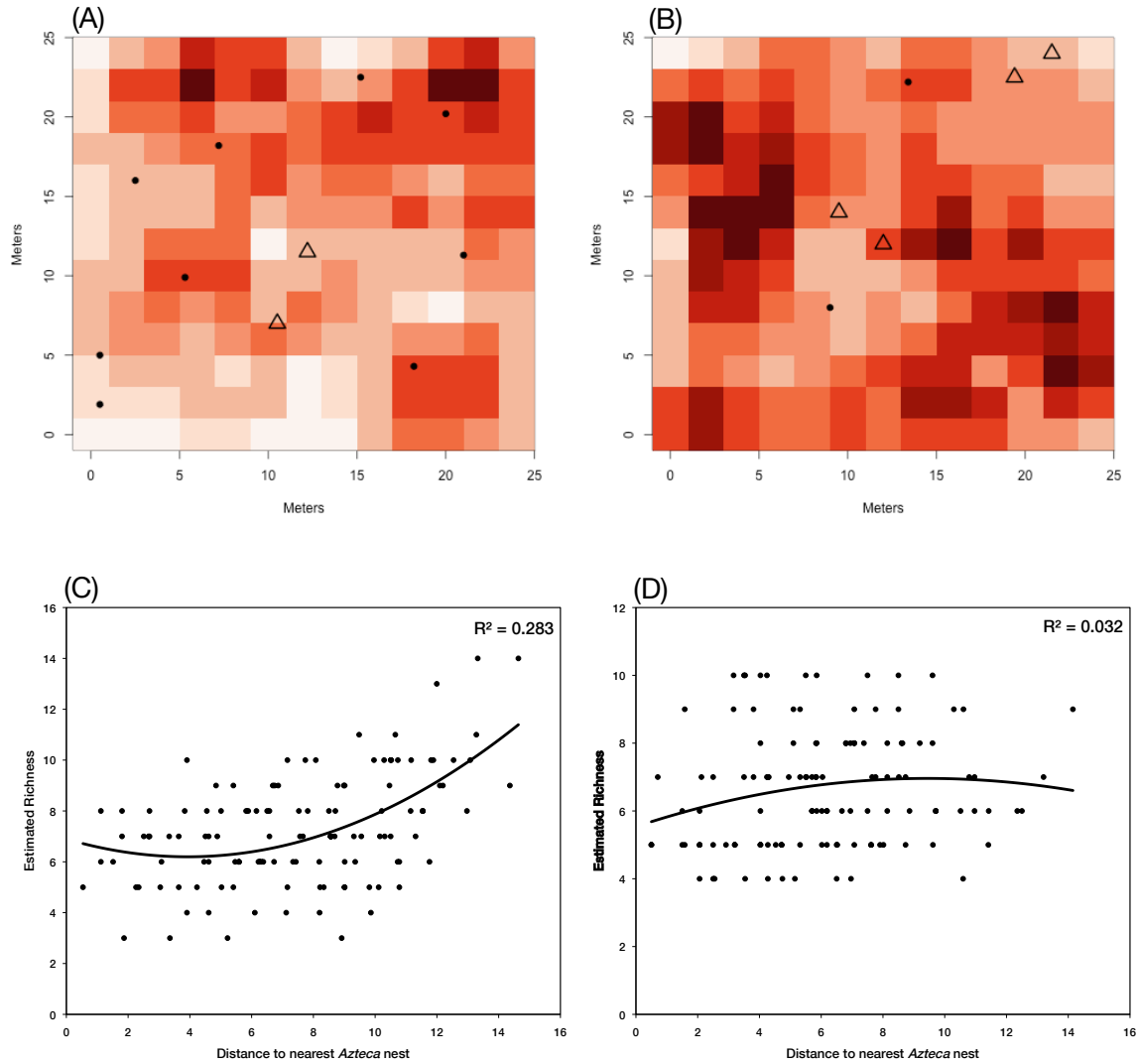
Figure 8. (A)-(B) Spatially explicit representations of results from ground-foraging ant surveys in low shade plots: (A) Plot R and (B) Plot P. Each sampling point (every 2m) is represented by a red colored square with the shade of the square indicating the number of ground-foraging ant morphospecies present. Darker red indicates a higher number of morphospecies present. Small black dots represent shade trees in the plot. Small black triangles represent shade trees occupied by *Azteca instabilis*. (C)-(D) Regressions of the results above (A. R^2=0.222, P <0.0001;B. R^2= 0.023, P =0.098). Each point represents a bait within (C) Plot R, (D) Plot P. The number of ground-foraging ant species increases with increasing distance from the nearest *Azteca* nest in (C) Plot R, but has no clear relationship in (D) Plot P. Each point represents a sampling point within (C) Plot R, (D) Plot P.
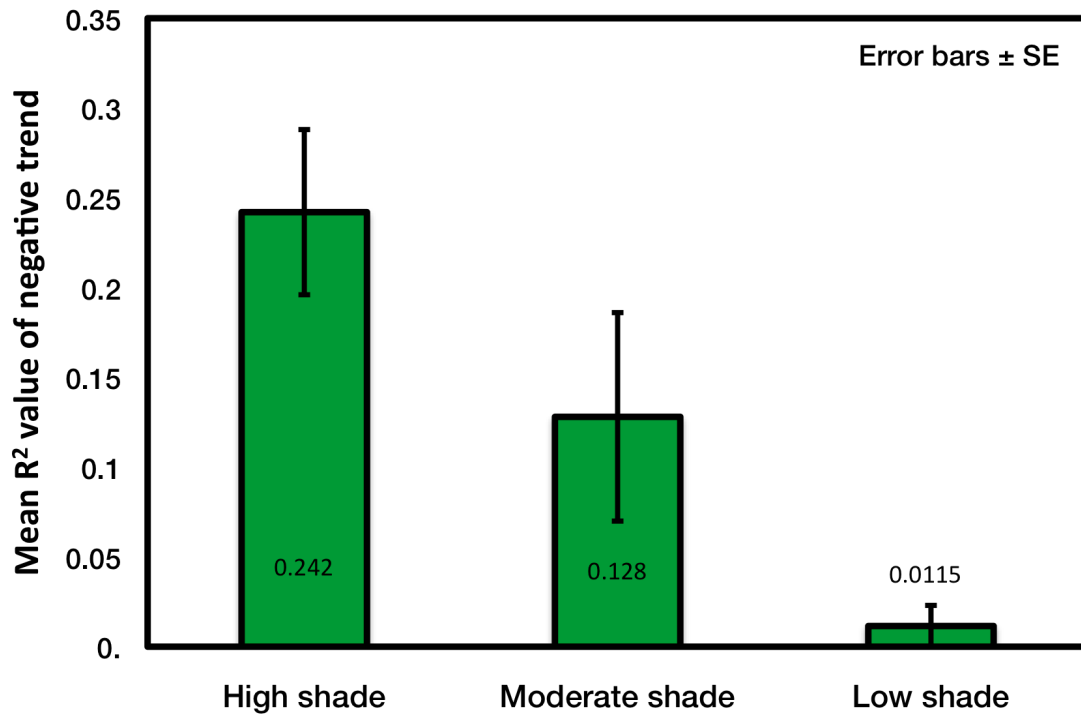
Figure 9. Mean R^2 value of the plotss in high shade, moderate shade and low shade for negative relationships between estimated species richness and distance to the nearest *Azteca* nest. Error bars represent ± SE.
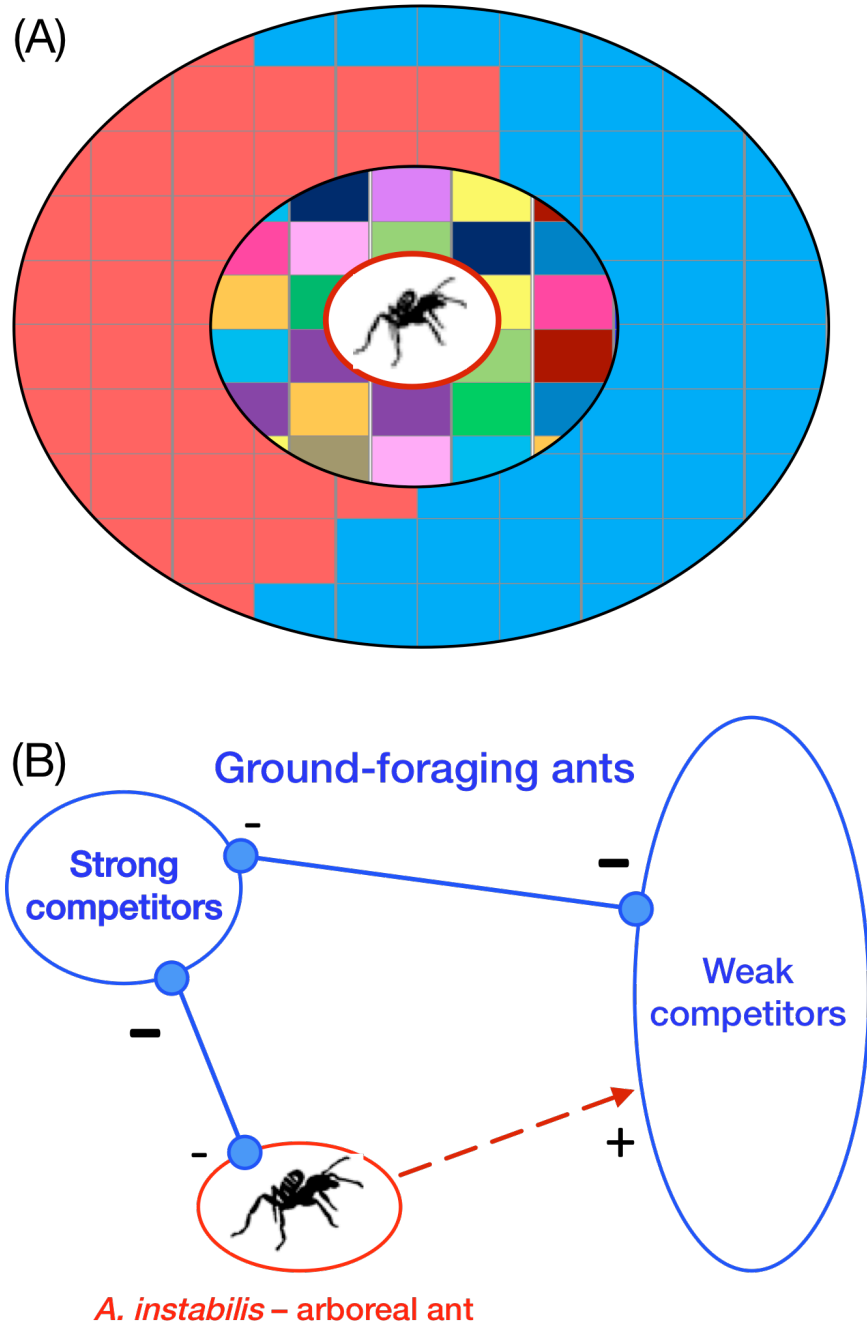
Figure 10. Two graphic representations of hypothesized interactions between *A. instabilis* and the ground-foraging ant assemblage. In (A) the background red and blue squares represent the ant mosaic produced by the strong competitors in the ground-foraging ant assemblage. The red circle around the image of *A. instabilis* represents the area of influence around a shade tree occupied by *A. instabilis*. The multicolored squares represent the 'zone of indeterminant competition' where weaker competitors in the ground-foraging ant assemblage can persist. (B) is an interaction diagram of the graphic in (A). Negative interactions are shown in circles and positive interactions are shown in red. Solid lines represent direct interactions and dotted lines represent indirect interactions. Larger negative symbols (-) represent a stronger negative effect.
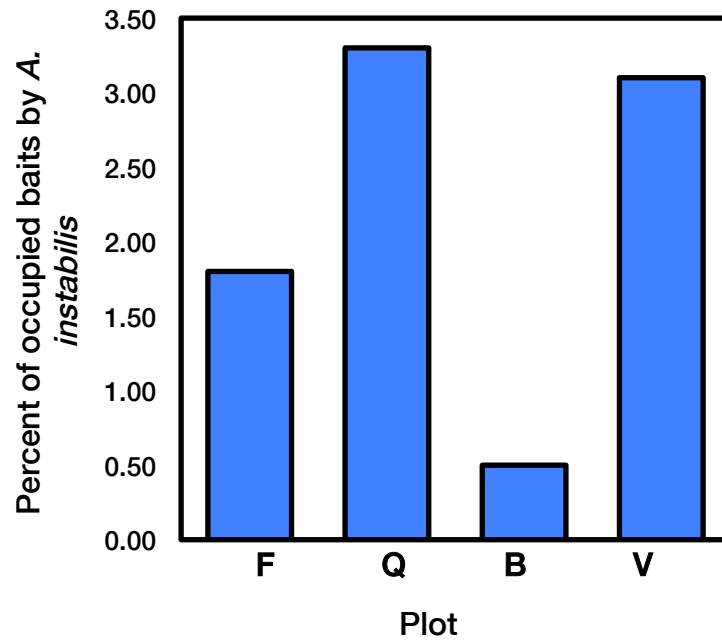
Figure 11. A comparison of the percent of occupied baits by *A. instabilis* in the four moderate shade plots. Plot B has the lowest percent of baits occupied by *A. instabilis*. This suggests that the linear relationship seen in the results may be due to the low presence of *A. instabilis* on the baits.

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