

INTERSPECIFIC SPACING BETWEEN HARVESTER ANT  
(*POGONOMYRMEX BARBATUS*) AND RED IMPORTED  
FIRE ANT (*SOLENOPSIS INVICTA*) COLONIES  
ALONG THE INVASION GRADIENT  
IN TEXAS

by

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## ABSTRACT

Invasive species can be devastating to ecosystems and their impacts on native species are innumerable. The red imported fire ant (*Solenopsis invicta*) invasion is a threat to many native species and is one hypothesized explanation for the observed decrease in the red harvester ant (*Pogonomyrmex barbatus*) within *S. invicta*'s invaded range. Understanding how *S. invicta* affects harvester ants is important given harvester ants' beneficial role in ecosystems and as prey for certain species. In this study I performed a "space for time substitution" to investigate temporal changes in the ecological interaction between these two species. The goal of my study was to quantitatively characterize the interaction and assess differences across *S. invicta*'s invasion gradient in Texas using data on interspecific spacing between *P. barbatus* and *S. invicta* colonies and density of *S. invicta* colonies in the vicinity of *P. barbatus* colonies (compared to neighboring points without colonies). I predicted that interspecific spacing would increase with time since first contact if *P. barbatus* colonies have developed an avoidance response. I obtained data for 125 *P. barbatus* colonies at 24 study sites. There was no difference in the spatial interaction between the two species along the invasion gradient. However, my results suggest there is possibly coexistence without an adaptive avoidance response by *P. barbatus*. Colony size of *P. barbatus* decreases as the density of fire ant mound increase; however, shorter distances between the species increases *P. barbatus* colony size. This result may represent a relatively intricate interaction worthy of future research. Overall my results indicate that *S. invicta* may not negatively impact *P.*

*barbatus* to the extent commonly thought, although *S. invicta* likely remains a threat to other native species.

## I. INTRODUCTION

Ecological invasions are an incredibly interesting but devastating threat to ecosystems and biodiversity worldwide. As many as 54% of recently recorded species extinctions were caused, at least in part, by invasive species (Clavero and Garcia-Berthou 2005). The impacts invasive species can have on native species and ecosystems are innumerable, but two of the most common are direct predation and competition for resources. Direct predation from invasive species as a cause of population declines in native species is commonly observed on islands where humans have introduced dogs, cats, rats, pigs, and mongooses (Henderson 1992; Aguirre-Munoz et al. 2008; Bonnaud 2010). These introduced animals prey on native species that have little or no evolutionary defenses to these alien threats. As the invasive species' population increases there is a decrease in the native species' population due to the increased predation pressure.

Declines in native species due to resource competition with invasive species is less obvious than predation and depends on the resource requirements of both the invader and native species. One example that is most relevant to this study is competition for space. Sessile organisms stay in one place throughout their lives (or at least move relatively little), so to thrive these organisms need an optimal location to settle. Invasive species that compete for space with native sessile organisms outcompete them in most cases because of a myriad of factors, resulting in the decline of the native species (Sakai et al. 2001).

In this study I investigated the interaction between the invasive red imported fire ant (*Solenopsis invicta*) and the red harvester ant (*Pogonomyrmex barbatus*). This interaction may represent direct interference competition in the form of aggression of fire



ants toward harvester ants and possibly some form of resource competition for space (Hook and Porter 1990; Porter and Salvignano 1990). Regardless of the exact form of the interaction, the expected outcome is that fire ants could be displacing harvester ants causing their local extinction. Alternatively, local coexistence may occur at sites where the harvester ants are able to establish their colonies at a sufficient distance from fire ant colonies. These ecological outcomes have not been previously studied for the harvester ant-fire ant interaction, particularly with regards to colony spacing. An important aspect of this interaction is that fire ants relocate their nest site (i.e., the mound or colony) frequently whereas harvester ants do not. Thus, fire ant colonies are spatially and temporally dynamic whereas the colonies of harvester ants are static (sessile) in comparison.

### Red Harvester Ant

There are several species of harvester ant that inhabit Texas, but *Pogonomyrmex barbatus* is the one species that is present throughout the state (Tabor 1998). This species of harvester ant like many others in the *Pogonomyrmex* genus forms “discs” that are circular clearings above their underground nests. The discs can reach between 1-2 meters in diameter as the ants actively remove vegetation leaving the soil exposed (McIntyre 2003; Figure 1). *Pogonomyrmex barbatus* also clears paths (“trunk trails”) that worker ants travel upon to more easily access foraging locations (Tabor 1998). Harvester ants received this common name because their main food source are seeds that the worker ants “harvest” from grasses and other plants and bring back to the colony for consumption (MacMahon et al. 2000). Individual worker *P. barbatus* are quite large compared to other ant species reaching between 7.0-9.5 mm in size (Tabor 1998). This species also has a

reddish rusty brown coloration that has led to it being given the common name “red harvester ant” or more simply the “red ant” (Figure 2). Colonies of *P. barbatus* form around an individual queen that can live between 15-20 years (Gordon 1991). After five years a *P. barbatus* colony becomes mature and maintains a population of approximately 10,000-12,000 individuals that form deep complex underground tunnel systems (Volny et al. 2006). *Pogonomyrmex barbatus* is abundant, but in certain areas of Texas there has been a decline in their density. Competition with the red imported fire ant (*Solenopsis invicta*) is one hypothesized explanation for the decline of *P. barbatus* (Hook and Porter 1990; Cook 2003; Quezada-Martinez et al. 2011).

### Red Imported Fire Ant

*Solenopsis invicta* was accidentally introduced to the United States at Mobile, Alabama from its native range in South America in the early 1930’s. Since then *S. invicta* has increased in number in the United States and has dispersed across a large area in the southern states (Fitzpatrick et al. 2007). As the *S. invicta* invasion front expanded it eventually reached the easternmost part of Texas in 1958, and began spreading across the state (Cokendolpher and Philips 1989). According to the United States Department of Agriculture (USDA), *S. invicta* has become established throughout the state except for the most northern counties in the panhandle and counties in far west Texas (Figure 3). *Solenopsis invicta* is smaller than *P. barbatus*, and colonies of the former are easily identified because of the fire ant’s coloration, appearance of the colony’s mound, and aggressive defensive response when the mound is disturbed. *S. invicta* build mounds that are domed up several centimeters from the ground and composed of loose soil collected from tunnel excavations. New colonies can be identified at about 6 months when their

mound size reaches 7-15 cm in diameter and 3-6 cm tall. Newly identifiable colonies can grow to reach 30-50 cm in diameter, 35 cm in height, and contain 200,000-400,000 individuals (Vinson 1997). *Solenopsis invicta* colonies are known to move their mounds frequently, anywhere from 1-30 m within a few days, but whether a colony remains in one location for many years or moves often depends on resource availability and environmental conditions (Favorite 1958; Lofgren et al. 1975; Vinson 1997). When a mound is disturbed thousands of the small red and black worker ants aggressively swarm and attack any object that is near their nest (Figure 4). *Solenopsis invicta* is omnivorous, but generally prefers to consume insects or other animal matter with only a small part of its diet consisting of seeds (Lofgren et al. 1975).

#### Interaction between Ants

It is generally believed that when *S. invicta* and *P. barbatus* inhabit the same area, *S. invicta* cause a decline in the *P. barbatus* population. Observations by Hook and Porter (1990) at the Brackenridge Field Laboratory in Austin, Texas described in detail the process by which a *P. barbatus* colony was actively attacked by *S. invicta* to the point at which the *P. barbatus* colony was completely destroyed. In that study the majority of the decline in *P. barbatus* occurred within one week, however complete colony destruction took 6-7 weeks. Another study in the same location was conducted to compare the arthropod biodiversity and abundance before and after *S. invicta* invaded the area. The results suggested that both overall arthropod biodiversity and abundance of many arthropod species decreased as numbers of *S. invicta* increased (Porter and Savignano 1990). Additionally other studies were conducted in other areas within *S. invicta*'s

invaded range that suggest various ant species decrease post *S. invicta* invasion (Cook 2003; Quezada-Martínez et al. 2011).

Time since invasion also may be an important factor to consider when assessing the impact that *S. invicta* has on ecosystems and other arthropod species. Nine years after the Porter and Savignano (1990) study a follow-up study was conducted by Morrison (2002) in which the results suggested that populations of many of the arthropod species severely affected by the initial *S. invicta* invasion were able to recover to pre-invasion levels. However, despite the widespread belief that *S. invicta* has a severe negative impact on *P. barbatus*, to my knowledge these studies are the only ones that have attempted to assess this impact.

#### Goal of the Study

Given the relative lack of knowledge about the interaction between harvester ants and fire ants, the goal of my study was to quantitatively characterize the interaction between the two species and assess if there are differences across the invasion gradient. I used data on interspecific spacing between *P. barbatus* and *S. invicta* colonies and density of *S. invicta* colonies in the vicinity of *P. barbatus* colonies to characterize the interaction. I examined the influence of colony spacing on species coexistence, that is, if harvester ant colonies are far enough away from fire ant colonies then perhaps harvester ant persistence is more likely. Alternatively, given that fire ant colonies (mounds) are more mobile than harvester ant colonies, it may not be possible for harvester ants to continually avoid fire ants. Assuming that the fire ants are more aggressive toward harvester ants (than vice-versa) then long-term persistence of harvester ants in the

presence of fire ants may not be possible. Lastly, perhaps colonies of harvester ants and fire ants are capable of coexisting in relatively close proximity.

### Research Questions

The main research questions for my study are listed below:

(1) Is there *non-random spacing* between harvester ant colonies and fire ant colonies?

That is, do the straight-line distances between harvester ant colonies and the nearest fire ant colonies differ from the distances between comparison points (lacking harvester ant colonies) and the nearest fire ant colonies?

(2) Are harvester ant colonies surrounded by a *higher or lower density* of fire ant colonies? That is, does the local “neighborhood” density of fire ant colonies around a harvester ant colony differ from that around comparison points?

(3) With regard to (1) and (2), is there any kind of differential response from *P. barbatus* to the *S. invicta* invasion (are there differences along the southeast to northwest invasion gradient)? If *S. invicta* does have an adverse effect on the survival of *P. barbatus* colonies then for coexistence to occur there must be some type of spatial separation between the species that limits their interaction. An adaptive response by *P. barbatus* to relocate colonies away from *S. invicta* would reduce the density and increase the distance of *S. invicta* around *P. barbatus* colonies, and hence mitigate any negative effect of *S. invicta* on *P. barbatus*. Of course there may be limited scope for this mechanism if *P. barbatus* colonies are not easily relocated. Also, smaller less active *P. barbatus* colonies would encounter *S. invicta* less often, so size of *P. barbatus* colonies and number of trunk trails might decrease with increasing amount of contact time (post-invasion) with *S. invicta*. I

expected to see *P. barbatus* colonies that have been exposed to *S. invicta* for a longer period of time to exhibit one or more of these responses that facilitate coexistence, as compared to colonies that have been exposed for a shorter amount of time.

(4) Does the size of a harvester ant colony (area of disc) and number of trunk trails differ based on distance to and density of fire ant colonies?

## II. METHODS

I used a “space for time substitution” to assess temporal changes in the ecological interactions (i.e., colony spacing dynamics) between *P. barbatus* and *S. invicta*. Because of how *S. invicta*’s invasion front has moved westward across the state since it was first recorded in 1953, *P. barbatus* in eastern and coastal Texas have been in contact with the invader for a greater period of time (Cokendolpher and Phillips 1989). Therefore, populations of *P. barbatus* in those regions should exhibit different interspecific spacing patterns than populations from central and west Texas, if there is an adaptive response occurring in *P. barbatus*. I collected data on colony spacing at 24 study sites located along a southeast to northwest gradient spanning 543 km from the most southeastern to most northwestern study sites (Figure 5).

I located *P. barbatus* colonies at the pre-selected study sites (e.g., state parks, city and county recreational areas). Study sites were intentionally selected to provide thorough coverage throughout the invaded region. To locate these study sites, I communicated with the public and biology professionals to identify public and private lands that I could access. I included no more than 21 harvester ant colonies from any single study site. In addition, at each study site I attempted to determine if there was any deliberate (anthropogenic) control of fire ants, particularly if the colonies appeared to be near areas of human recreational use.

For each *P. barbatus* colony I measured several variables (Table 1). When a *P. barbatus* colony was discovered, I first recorded its GPS location (latitude and longitude). Then I determined the size of the colony by measuring the colony’s width in two locations, one at the widest diameter and another perpendicular to that line. I then

averaged these two measurements and took that as the diameter in the calculation of disc area (assuming the disc was well-approximated as a circle). After that, I recorded ant activity level, extent of cloudiness, and ground surface temperature. Activity level was recorded as the number of ants present on the mound's cleared disc in increments of 50 individuals. Ground temperature and cloud cover might influence activity level in *P. barbatus* (Box 1960; Whitford and Ettershank 1975), hence the need to obtain and record those data. I measured ground temperature with a laser thermometer pointed near the entrance of the colony and cloud cover was recorded in one of three categories (full sun, partly cloudy, total cloud cover). I also recorded the number of trunk trails cleared by the colony. Finally, I measured the distance from the entrance of the *P. barbatus* colony to the edge of the nearest *S. invicta* colony (distances  $\geq 20$  m were recorded as 20) and counted all the *S. invicta* colonies (mounds) within a 10 m radius of the *P. barbatus* colony (up to a maximum of 10 mounds). The limits of 20 m and 10 mounds allowed for more efficient data collection, although these limits were rarely realized, only 17.8 and 3.8% of the observations respectively. I also collected the data for distance to nearest *S. invicta* colony and number of *S. invicta* mounds within 10 m for three comparison points (degree headings of 0° north, 120° southeast, and 240° southwest) that were each 20 m from the entrance of the *P. barbatus* colony (Figure 6). The distance of 20 m was used because it corresponds to the furthest mean intraspecific spacing between *P. barbatus* colonies in the literature (Holldobler 1974; Gordon 1991). Each harvester ant colony (disc) was photographed for a permanent record of the surrounding vegetation. I assessed the general habitat for the area around each *P. barbatus* colony and comparison points based on which habitat occupied the majority of the space and recorded them in one of



six categories: bare ground, rock, short grass (< 50 cm), tall grass (> 50 cm), scrub, and trees. I then compared the mean values of distance to nearest *S. invicta* colony and number of *S. invicta* mounds among the different habitat types, and conducted a chi-square test to determine if the habitats of *P. barbatus* colonies differed from those of comparison points.

From each *P. barbatus* colony I collected 3-6 individual ants and stored them in 70% ethanol for later verification of species (although upon collection, all colonies were suspected of being *P. barbatus*). My main dataset consisted of 125 harvester ant colonies visited a single time.

For each harvester ant colony, I calculated an index of spatial association with fire ant colonies as  $A = [(X_{com} - X_{har}) + (D_{har} - D_{com}) \times 2] \times 0.025$ , where  $X_{com}$  is the average distance between each of the three comparison points and its nearest fire ant mound,  $X_{har}$  is the distance between the harvester ant colony and closest fire ant mound,  $D_{har}$  is the density of fire ant mounds within 10 m of the harvester ant colony, and  $D_{com}$  is the average density of fire ant mounds within 10 m of the comparison points. Because the distance data are bounded between 0 and 20 m the term  $X_{com} - X_{har}$  varies between -20 and +20. Similarly, density data are bounded between 0 and 10, hence  $D_{har} - D_{com}$  varies between -10 and +10. Multiplying by 2 puts this term on the same scale as  $X_{com} - X_{har}$ . Multiplying by 0.025 rescales  $A$  to range between -1 and +1, where low negative values represent a negative spatial association of harvester ant colonies with fire ants and high positive values represent a positive association, relative to the comparison points.

Research Question 1 was addressed by comparing  $X_{har}$  to  $X_{com}$  for individual *P. barbatus* colonies as well as “groups” of colonies representing study sites and the entire

set of colonies. For each group, I calculated the mean value of  $X_{com} - X_{har}$  over all colonies and used a 2-tailed  $t$ -test to determine if the mean was significantly different from 0. Additionally, different groups (e.g., representing different study sites) were compared using two-sample  $t$ -tests and ANOVA. Likewise, Question 2 was addressed with the same tests, but instead using  $D_{har} - D_{com}$  as the response variable. Question 3 was tested by performing a multiple regression and several simple linear regressions of the spatial association index ( $A$ ) regressed against longitude, latitude, disc area, activity level of the colony, and number of trunk trails. Lastly, Question 4 was examined using a multiple regression and a series of simple linear regressions to test for a relationship among size of *P. barbatus* colony (area of the disc), activity level (number of individuals on disc surface), and number of trunk trails as the response variables and  $X_{har}$  and  $D_{har}$  as predictor variables.

Although my study was primarily intended to examine differences in the harvester ant and fire ant interaction along a spatial gradient, I also collected data for a temporal analysis. I compiled an additional dataset that consisted of five repeat visits to eight harvester ant colonies located at a single site near San Marcos. These repeat visits occurred from September 2017 to June 2018 with successive visits typically a few weeks to a couple of months apart. For these colonies and paired comparison points, I collected data on distance to and densities of fire ant mounds as described above for the set of 125 colonies. The purpose of the repeat visits was to assess the extent to which fire ants were spatially and temporally dynamic around harvester ant colonies in relation to the comparison points. For each colony I calculated the minimum, maximum, and mean values of  $X_{har}$  and  $D_{har}$  over the five repeat visits and the minimum, maximum, and mean

$X_{com}$  and  $D_{com}$  values for the comparison points. To more directly measure temporal variation in these four variables I also calculated the sum of absolute changes (for example, the temporal series of 2/4/1/2/5 has a sum of absolute change = 9) for each of the variables; i.e., this was the fifth variable. I then used  $t$ -tests to compare the mean values of these five variables between the *P. barbatus* colonies and the comparison points.

### III. RESULTS

Among all 125 *P. barbatus* colonies, distance to nearest fire ant mound ( $X_{har}$ ) ranged from 0.42 to 20 m with mean = 7.76 m. Number of fire ant mounds within 10 m ( $D_{har}$ ) ranged from 0 to 10 with mean = 2.43. Among all 375 comparison points, distance to nearest fire ant mound ( $X_{com}$ ) ranged from 0.31 to 20 m with mean = 8.67 m. Number of fire ant mounds within 10 m ( $D_{com}$ ) ranged from 0 to 10 with mean = 2.33. The spatial association index ( $A$ ) ranged from -0.43 to 0.54 with mean  $A = 0.03$  which was not significantly different from 0 (one-sample  $t$ -test;  $t = 1.48$ ,  $P = 0.14$ ). Additionally  $A$  did not differ along the southeast to northwest invasion gradient of *S. invicta* (Figure 7). That is,  $A$  was not significantly related to longitude ( $t = 0.53$ ,  $R^2 = 0.002$ ,  $P = 0.60$ ) or latitude ( $t = 0.51$ ,  $R^2 = 0.002$ ,  $P = 0.61$ ). Also, neither of the components of  $A$ , namely  $X_{com} - X_{har}$  and  $D_{har} - D_{com}$ , were influenced by longitude or latitude ( $P > 0.05$  for all four regressions). There was also no significant relationship between  $A$  and disc area ( $t = 0.001$ ,  $R^2 < 0.001$ ,  $P = 0.99$ ), activity level ( $t = -0.09$ ,  $R^2 < 0.001$ ,  $P = 0.93$ ), number of truck trails ( $t = -0.61$ ,  $R^2 = 0.003$ ,  $P = 0.54$ ), or the combination of these predictor variables ( $F_{5,119} = 0.15$ ,  $R^2 < 0.001$ ,  $P = 0.98$ ). These results indicate that the spatial association between *P. barbatus* and *S. invicta* colonies was not significantly affected by any of these predictor variables.

Despite neither latitude nor longitude affecting the spatial association between *P. barbatus* and *S. invicta* colonies, there could still be differences among and within sites in regards to spatial pattern. Therefore I conducted a one-way ANOVA on  $X_{har} - X_{com}$  and on  $D_{har} - D_{com}$  with “site” as the grouping variable in both ANOVAs. When comparing sites that have at least 8 colonies sampled there were no significant differences among the

sites in either  $X_{har} - X_{com}$  ( $F_{7,80} = 0.29$ ,  $P = 0.96$ ; Figure 8) or  $D_{har} - D_{com}$  ( $F_{7,80} = 1.23$ ,  $P = 0.30$ ; Figure 9). However, comparisons within a site revealed a marginally significant difference between  $X_{har}$  and  $X_{com}$  (mean difference = -1.77 m,  $t = -2.14$ ,  $P = 0.06$ ) and between  $D_{har}$  and  $D_{com}$  (mean difference = 1.4 fire ant mounds,  $t = 2.07$ ,  $P = 0.06$ ) at site Z (San Angelo). There was also a significant difference between  $D_{har}$  and  $D_{com}$  (mean difference = -0.83 fire ant mounds,  $t = -2.50$ ,  $P = 0.04$ ) at site E (College Station). No other sites had a significant difference between  $D_{har}$  and  $D_{com}$  or between  $X_{har}$  and  $X_{com}$ . Further, when all sites were combined, there was a marginally significant difference between  $X_{har}$  and  $X_{com}$  (mean difference = -0.90 m,  $t = -1.85$ ,  $P = 0.07$ ) but no significant difference between  $D_{har}$  and  $D_{com}$  (mean difference = 0.11 fire ant mounds,  $t = 0.57$ ,  $P = 0.57$ ).

Although disc area, number of trunk trails, and ant activity level did not have a significant effect on the spatial association index, these variables themselves could be affected by proximity of fire ants in that each is essentially a measure of the size and behavior of the *P. barbatus* colony. Therefore I conducted a series of one-factor regressions assessing the relationship between each of the above variables and  $X_{har}$  and  $D_{har}$ . Disc area was significantly related to  $X_{har}$  and  $D_{har}$ , number of trunk trails and ant activity level were not significantly related to distance to fire ant mounds and density of fire ant mounds (Table 2). For every 1 m increase in distance to nearest *S. invicta* mound there was a decrease in disc area of 0.11 m<sup>2</sup> and for each additional *S. invicta* mound (within 10 m) there was a decrease in disc area of 0.23 m<sup>2</sup>. Thus, distance to nearest *S. invicta* mound and density of mounds had opposite effects on disc area of *P. barbatus*.

colonies. As expected, I was also able to demonstrate that the number of *P. barbatus* individuals on the disc of a colony (activity level) is related to the disc's area (Figure 10).

Comparing the mean values of  $X_{har}$ ,  $D_{har}$ ,  $X_{com}$ , and  $D_{com}$  revealed that there was no difference between *P. barbatus* colonies and comparison points within any of the six habitat types (Table 3). There was also no difference between *P. barbatus* colonies and comparison points with regard to their frequencies in the different habitat types ( $\chi^2 = 2.60$ ,  $P = 0.24$ , Figure 11). Short grass was the predominant vegetation type around *P. barbatus* colonies and comparison points (Figure 11). Additionally the vast majority of *P. barbatus* colonies and comparison points were located in open areas (all habitat types except trees and scrub; 96.80% and 92.53% of colonies and comparison points respectively). This indicates that most of the sampled *P. barbatus* colonies were in open areas with more open area nearby.

The assessment of the temporal aspect of the *P. barbatus* – *S. invicta* interaction did not reveal any significant differences between *P. barbatus* colonies and comparison points (Table 4). The number of fire ant mounds within 10 m of *P. barbatus* colonies ( $D_{har}$ ) and distance to the closest fire ant mound ( $X_{har}$ ) both varied at each colony (and on average over all eight colonies) during the 10-month period but the variability was no greater than that expressed at the comparison points. Nonetheless this assessment does demonstrate that *S. invicta* mound formation at the study sites is dynamic spatially and temporally in that the number of mounds fluctuated with mounds appearing and disappearing as indicated by changes in the distance to nearest fire ant mound relative to either *P. barbatus* colonies or comparison points (Table 4).

#### IV. DISCUSSION

To my knowledge this study is the only one which has sought to determine the impact of *S. invicta* on *P. barbatus* colonies across a scale as large as the invasion gradient in Texas (Figure 5). Other studies of the *P. barbatus* – *S. invicta* interaction focused on one general area or study location (Hook and Porter 1990; Porter Savignano 1990; Cook 2003; Morrison 2002; Quezada-Martínez et al. 2011). The scale of my study provides unique knowledge about these two species' interaction that has not been provided by other studies. Along the entire invasion gradient, there was no significant difference in the index of special association ( $A$ ), the distance between the two species compared to comparison points ( $X_{har} - X_{com}$ ), and the density of *S. invicta* mounds near *P. barbatus* colonies compared to comparison points ( $D_{har} - D_{com}$ ). These variables were not related to latitude or longitude. These results indicate that *S. invicta* may not have as severe an impact on *P. barbatus* as is commonly thought, at least with regard to the coexistence of the two species on a relatively fine spatial scale (Hook and Porter 1990; Cook 2003; Quezada-Martinez et al. 2011).

Despite the lack of a geographic (or time since contact) effect on the spacing of *P. barbatus* and *S. invicta* colonies, I was able to identify differences in spacing at specific locations within the invaded area. At an eastern study location (site E, Figure 5) there were on average 0.83 fewer *S. invicta* mounds within 10 m of *P. barbatus* colonies than surrounding comparison points. At a western study location (site Z, Figure 5) there were on average 1.4 more *S. invicta* mounds within 10 m of *P. barbatus* colonies and the *S. invicta* mounds were on average 1.77 m closer to the *P. barbatus* colonies than were surrounding comparison points; however the results for this location were only

marginally significant ( $0.05 < P < 0.1$ ). These results provide a small amount of support that *S. invicta* may be having a negative effect on *P. barbatus* at some areas within the invasion range although the amount of time in contact does not seem to be relevant overall. However, before making any premature conclusions from these data it is important to consider that these study sites had relatively small sample sizes (8 and 12 respectively for sites E and Z) and thus much greater sampling would be needed to conclusively demonstrate a negative effect of *S. invicta* on *P. barbatus* at these sites.

Although the interspecific spacing of *P. barbatus* and *S. invicta* colonies was not substantially different from random and apparently unrelated to time since contact, *S. invicta* might still affect (at least hypothetically) the size and behavior of *P. barbatus* colonies – therefore I examined this possibility. I did not find any significant relationships between either number of trunk trails or ant activity level regressed against distance to and density of *S. invicta* mounds. However, distance and density of *S. invicta* mounds did have a significant combined effect on disc area (Table 2). *P. barbatus* colonies nearer to *S. invicta* mounds tended to be larger in area although density of *S. invicta* mounds had the opposite effect on disc area. This finding is difficult to interpret in an ecological context because the two factors seem to conflict with each other. Perhaps fire ants can suppress growth of *P. barbatus* colonies and hence disc area when they are at high density in the area immediately around the colony and yet be attracted to (and thereby) closer to larger colonies (discs). Another explanation for this relationship could be that when *P. barbatus* clears vegetation and redistributes soil particles (thereby producing the disc), it creates a more disturbed (bare) habitat than the surrounding area, with larger colonies creating more disturbance and preferred nesting locations for *S.*



*invicta* (Wagner et al. 1997; MacMahon et al. 2000; Nicolai et al. 2008). Disturbed locations are favored by *S. invicta* and they are known to have higher mound densities in these areas compared to less disturbed areas (Stiles and Jones 1998; LeBrun et al. 2012; Tschinkel and King 2013). However, there may be a trade-off for *S. invicta* to establish near *P. barbatus* colonies because if their density becomes too high they may destroy the *P. barbatus* colony that in turn will result in the disappearance of the favorable habitat. In this scenario, there would be a limited and low density of relatively close *S. invicta* mounds (Hook and Porter 1990). More studies are needed to better assess this ecological explanation.

My study also revealed that the number of *P. barbatus* individuals on the disc of a colony (activity level) increases as the disc's area increases (Figure 10). As they get older, colonies tend to increase in number of individuals (Sanders and Gordon 2004; Volny et al. 2006). Thus, disc area is a good proxy variable for the number of *P. barbatus* individuals in a colony and presumably available to defend the colony. This could be important in that larger colonies might be able to better tolerate or withstand the close presence of *S. invicta*; this would also explain the inverse relationship between disc area and distance to nearest *S. invicta* mound.

The vast majority of *P. barbatus* colonies that I discovered and sampled were located in open areas (all habitat types except trees and scrub) with even more open area nearby. This is not a surprising result considering the number of studies that also show a "preference" or at least an association of *P. barbatus* with open habitat (Moody and Francke 1982; MacMahon et al. 2000; McIntyre 2003; Nicolai et al. 2008), however it should also be noted that I focused my search efforts in open habitat. Finally my study

demonstrated that *S. invicta* mound formation is dynamic spatially and temporally in that the number of mounds fluctuated with mounds appearing and disappearing as indicated by changes in the distance to nearest fire ant mound relative to either *P. barbatus* colonies or comparison points (Table 4). This indicates that *S. invicta* has the ability to move its colonies frequently, and provides additional support to other studies that make this observation (Favorite 1958; Lofgren et al. 1975; Vinson 1997).

*Pogonomyrmex barbatus* along with the other 29 species of “harvester ants” in North America (12 in Texas) are ecologically significant given that they have important and beneficial roles in many arid land ecosystems (Tabor 1998; MacMahon et al. 2000; Nicolai et al. 2008; Gosselin et al. 2016). When creating their colonies and the associated bare disc (in some species) harvester ants cycle nutrients up from several meters underground. This leads to more fertile soil in the immediate area around the colony (Wagner et al. 1997; MacMahon et al. 2000). In many cases this results in the vegetation composition around harvester ant colonies being different from the surrounding landscape, and may increase the vegetation’s resilience to environmental disturbance (Nicolai et al. 2008; Gosselin et al. 2016). Harvester ants are also a prey source for many species. Some species such as *P. barbatus*, *P. rugosus*, and *P. occidentalis* that create large, populous, and long-lived colonies can provide a reliable food source for many years. Animals such as mockingbirds, doves, shrikes, sand lizards, fence lizards, spadefoot toads, plains blind snake, assassin bugs, and black widows have all been known to prey on harvester ants (Tabor 1998). However, the most notable harvester ant predators are horned lizards. Texas horned lizards (*Phrynosoma cornutum*) are considered to be dietary specialists with between 69-90% of their diet consisting of

*Pogonomyrmex* harvester ants (Blackshear and Richerson 1999; McIntyre 2003).

Understanding how *S. invicta* affects harvester ants is important given harvester ant's beneficial role in ecosystems and as a prey base for certain species. The *S. invicta* invasion is a threat to many native species and is one hypothesized explanation for the observed decrease in harvester ants within *S. invicta*'s invaded range (Hook and Porter 1990; Cook 2003; Quezada-Martinez et al. 2011). However, contrary to some previous research (Hook and Porter 1990; Cook 2003; Quezada-Martinez et al. 2011), *S. invicta* may not be as detrimental to harvester ants as presently presumed. Although I have not demonstrated a significant beneficial relationship between the two species across the *S. invicta* invasion gradient, my study has provided some evidence for the possibility of coexistence without an adaptive avoidance response by *P. barbatus*. This could indicate that *S. invicta* may not negatively impact *P. barbatus* to the extent commonly thought, although fire ants likely remain a threat to other native species.

## APPENDIX SECTION

Table 1. Data and information collected for each harvester ant colony.

Data to be collected	Method of data collection	Use of data
Number of fire ant mounds within 10m	Circular area within 10 m of colony visually searched for fire ant mounds (max 10 recorded).	Calculation of the index of spatial association.
Distance to nearest fire ant mound	The straight-line distance from the entrance of the harvester ant mound to the outside edge of the nearest fire ant mound (to a maximum of 20 m).	Calculation of the index of spatial association.
Latitude and longitude	The GPS location of the harvester ant mound.	Analysis of a geographic effect on the spatial association between the two ant species.
Maximum width and perpendicular width	The width of the mound (cleared disc) at its widest length and the width of the line perpendicular to the widest axis.	Used to estimate disc area (size).
Number of trunk trails	The number of obvious cleared paths that radiate from the harvester ant colony.	Indicates foraging intensity and area foraged by the colony. Used in the analysis of colony spacing and disc size.
Activity level	The number of harvester ants on the surface of the mound at the time of data collection rounded to the nearest 50.	Indicates current activity number of individuals in colony. Used in the analysis of colony spacing and disc size.
Ground temperature	The temperature of the ground adjacent to the entrance of the harvester ant colony recorded using a laser thermometer.	Extraneous variable that could be needed to adjust the activity level variable.
Cloud Cover	The extent of cloudiness recorded as being sunny, partly cloudy, or cloudy.	Extraneous variable that could be needed to adjust the activity level variable.
Fire ant control	Fire ant control (yes or no) at the study site where harvester ant colony was located.	Information that could possibly assist in interpretation of spacing results.

Table 1 Continued. Data and information collected for each harvester ant colony.

Photograph	A photograph of the harvester ant mound and surrounding vegetation.	Vegetation height and general description to assign the habitat of colony to one of six categories.
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Table 2. Results from a series of one-factor regressions assessing the relationship between the distance between a focal *P. barbatus* colony and the nearest *S. invicta* mound ( $X_{har}$ ) and the density of *S. invicta* mounds within 10 m of a focal *P. barbatus* colony ( $D_{har}$ ) with disc area, trunk trail number, and activity level.

Response variable	Predictor	Regression coefficients	$t$	$R^2$	$P$
Disc area	$X_{har}$	-0.05	-1.66	0.02	0.10
	$D_{har}$	-0.05	-0.69	<0.01	0.49
	$X_{har} + D_{har}$	-0.11, -0.23	-2.37, -2.82	0.06	0.017
Trunk trail number	$X_{har}$	-0.03	-1.09	0.01	0.28
	$D_{har}$	-0.03	-0.36	<0.01	0.72
	$X_{har} + D_{har}$	-0.07, -0.135	-1.75, -1.41	0.025	0.21
Activity level	$X_{har}$	-0.12	7.54	<0.01	0.85
	$D_{har}$	-0.85	-0.53	<0.01	0.60
	$X_{har} + D_{har}$	-0.60, -1.80	-0.70, -0.86	<0.01	0.68

Table 3. Mean values for  $X_{har}$ ,  $X_{com}$ ,  $D_{har}$ , and  $D_{com}$  for the *P. barbatus* colonies ( $n = 125$ ) and comparison points ( $n = 375$ ) located in each habitat type. Values in parentheses are standard deviations.

Habitat Type	$N_{har}$	$N_{com}$	$X_{har}$	$X_{com}$	$D_{har}$	$D_{com}$
Bare ground	1	7	7.93 (na)	13.51 ( $\pm 6.36$ )	1 (na)	0.71 ( $\pm 1.50$ )
Rock	2	11	5.69 ( $\pm 3.73$ )	10.20 ( $\pm 6.16$ )	2 ( $\pm 0$ )	1.18 ( $\pm 1.78$ )
Scrub	3	21	20 ( $\pm 0$ )	15.36 ( $\pm 7.64$ )	0 ( $\pm 0$ )	0.52 ( $\pm 0.93$ )
Short grass	107	286	7.60 ( $\pm 6.37$ )	8.22 ( $\pm 6.56$ )	2.53 ( $\pm 2.69$ )	2.59 ( $\pm 2.75$ )
Tall grass	11	43	5.24 ( $\pm 2.71$ )	7.31 ( $\pm 6.41$ )	2.55 ( $\pm 2.11$ )	2.19 ( $\pm 1.98$ )
Trees	1	7	20 (na)	7.93 ( $\pm 6.18$ )	0 (na)	1 ( $\pm 0.82$ )

Table 4. Temporal assessment of the *P. barbatus* – *S. invicta* interaction based on minimum, maximum, mean, and sum of absolute change in  $X_{har}$ ,  $X_{com}$ ,  $D_{har}$ , and  $D_{com}$  calculated over the five repeat visits to a single study site near San Marcos, Texas. Values in table are means for the eight colonies ( $X_{har}$  and  $D_{har}$ ) or 24 comparison points ( $X_{com}$  and  $D_{com}$ ).

Comparison	<i>P. barbatus</i> colonies	Comparison points	<i>t</i>	<i>P</i>
Mean $X_{har}$ vs $X_{com}$	4.51	5.82	-2.11	0.07
Minimum $X_{har}$ vs. $X_{com}$	2.14	2.36	-0.34	0.74
Maximum $X_{har}$ vs. $X_{com}$	8.72	10.49	-1.22	0.26
Summed change $X_{har}$ vs. $X_{com}$	9.83	13.82	-1.42	0.20
Mean $D_{har}$ vs $D_{com}$	3.50	3.27	0.63	0.55
Minimum $D_{har}$ vs. $D_{com}$	1.75	0.88	2.23	0.06
Maximum $D_{har}$ vs. $D_{com}$	6.12	6.08	0.06	0.95
Summed change $D_{har}$ vs. $D_{com}$	9.38	9.04	0.20	0.85





**Figure 1.** *Pogonomyrmex barbatus* colony with obvious cleared “disc” area.



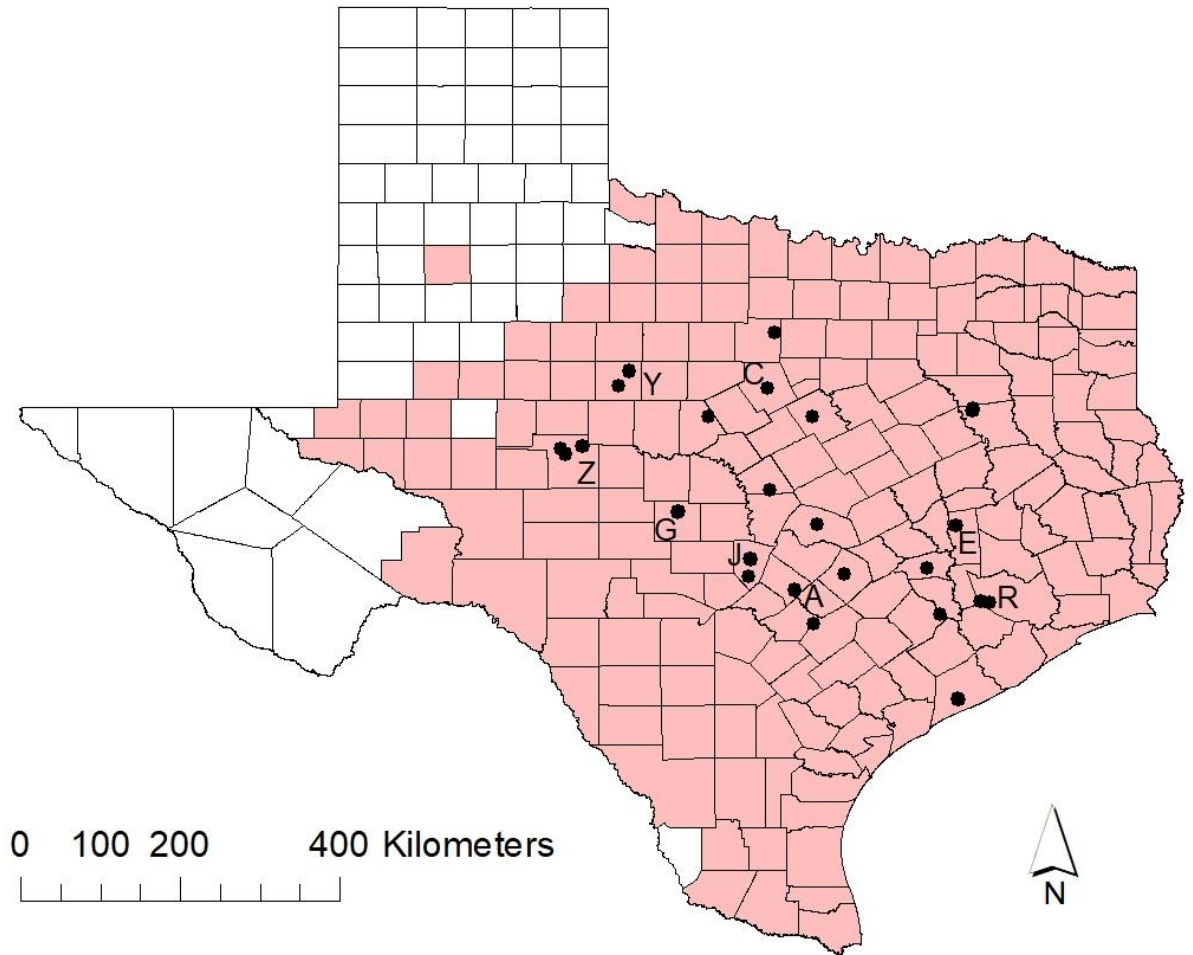
**Figure 2.** *Pogonomyrmex barbatus* workers showing the reddish coloration typical of the species. Image from <http://www.discoverlife.org/>.



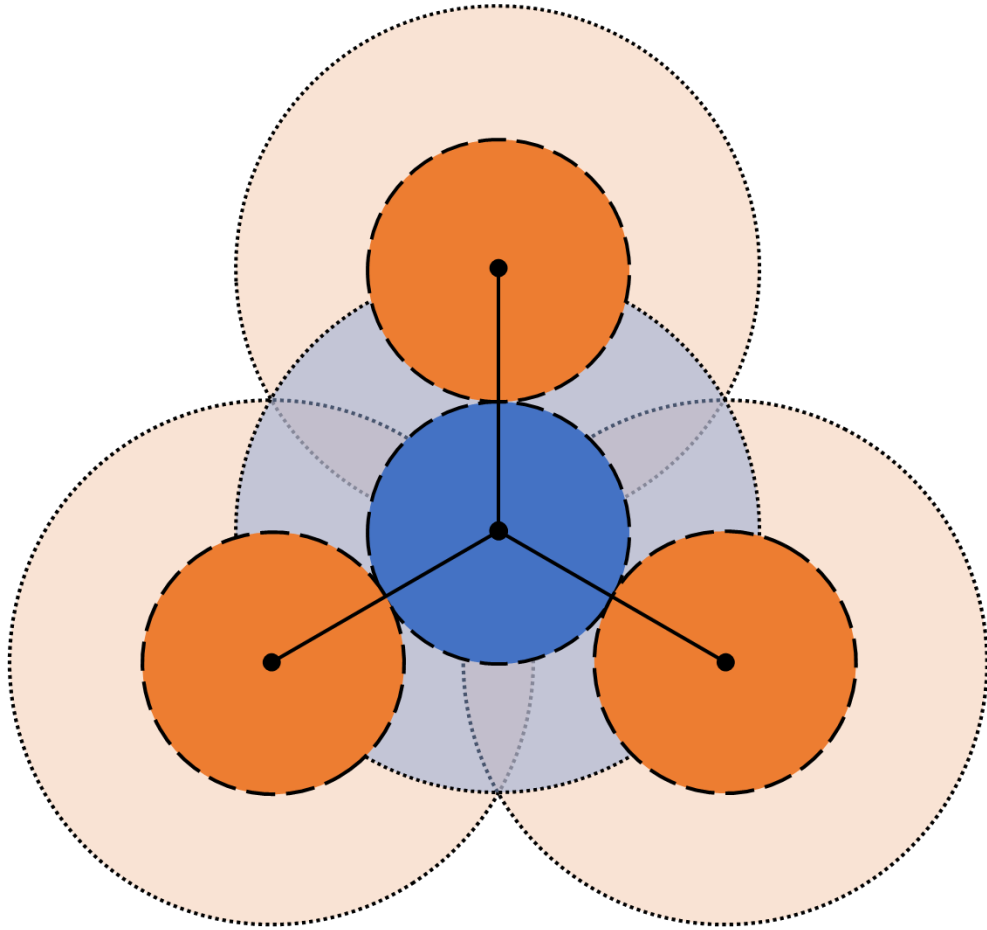
**Figure 3.** USDA map that shows counties in the USA in which *Solenopsis invicta* has become established as of June 2016. Image from <http://entopl.okstate.edu/fireants/>.



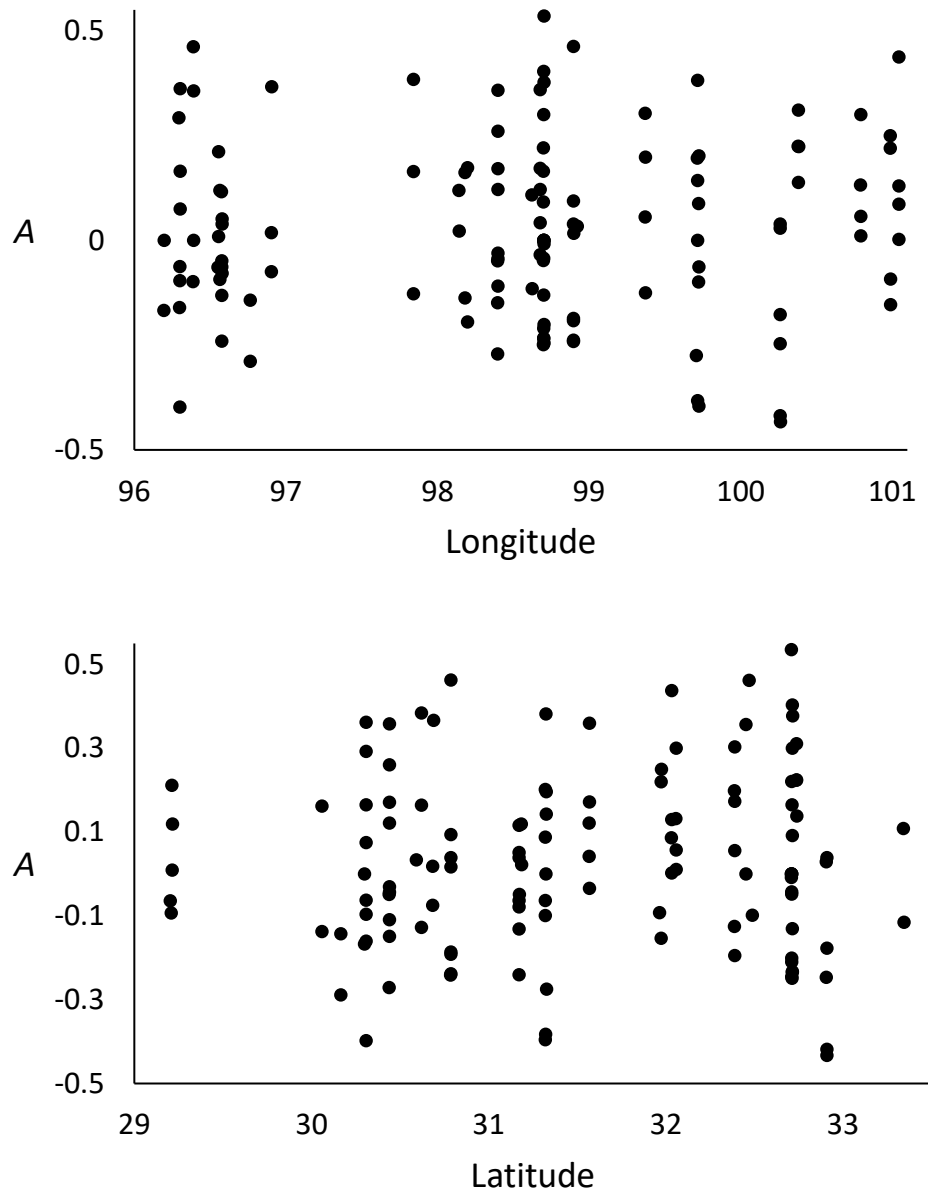
**Figure 4.** This image shows the black and red coloration of *Solenopsis invicta* and its behavior in aggressively swarming anything that disturbs its nest. Image from <http://bugguide.net/images/>.



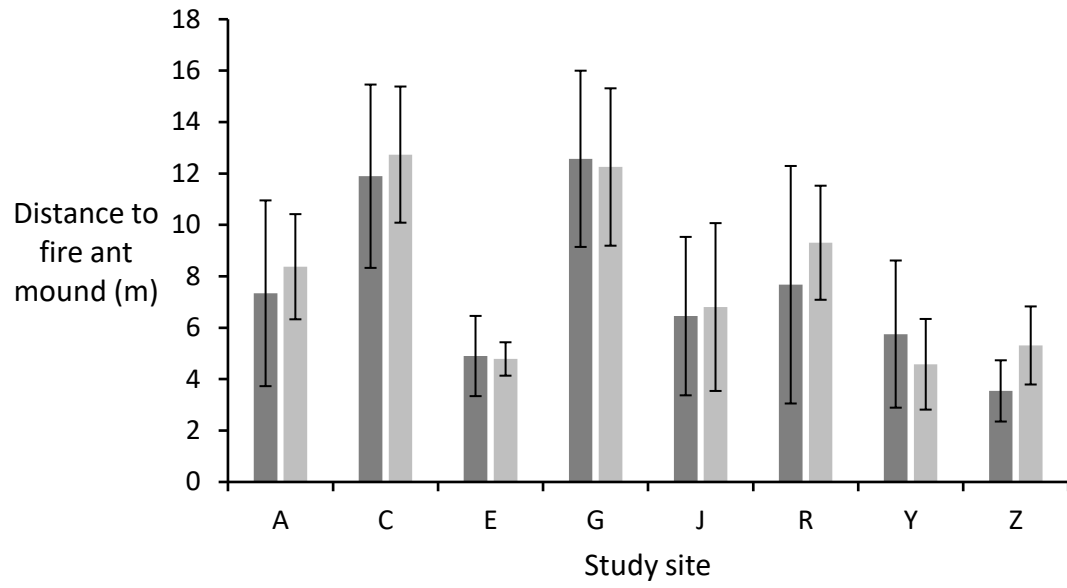
**Figure 5.** Map that shows the locations of *Pogonomyrmex barbatus* colonies sampled in this study as black points along with the counties that have confirmed *Solenopsis invicta* collection in red, as of October 2015 (McDonald et al. 2016). Study sights with at least eight *P. barbatus* colonies sampled are labeled as they are in Figures 8 and 9.



**Figure 6.** A visual representation of my survey method. The central point surrounded by blue circles represents the location of a *P. barbatus* colony, the three points surrounded by orange circles represent the comparison points. The solid lines connecting these points represent the 20 m path that I traveled to reach the comparison points. The smaller darker circles represent the 10 m radius in which I counted all the *S. invicta* mounds (up to a maximum of 10 mounds). The larger lighter circles represent the 20 m maximum distance I searched if no colonies were discovered within 10 m in order to measure the distance from the central point to the edge of the nearest *S. invicta* colony.

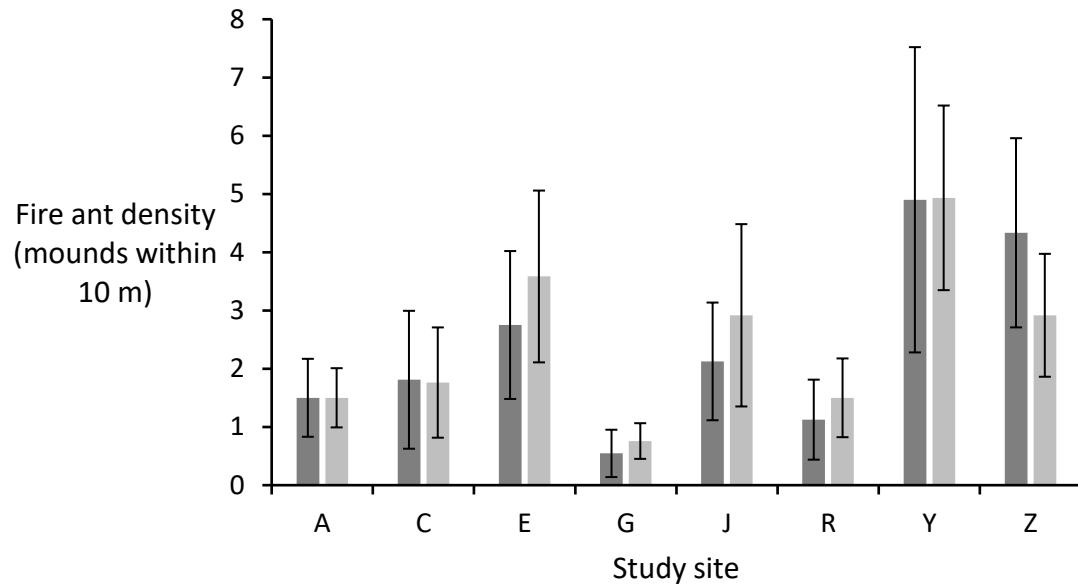


**Figure 7.** The lack of a relationship between the spatial association index ( $A$ ) with longitude and latitude of *P. barbatus* colonies.  $A$  is an index value from -1 to 1 representing the extent to which *P. barbatus* and *S. invicta* colonies are spatially associated (see text for more details).

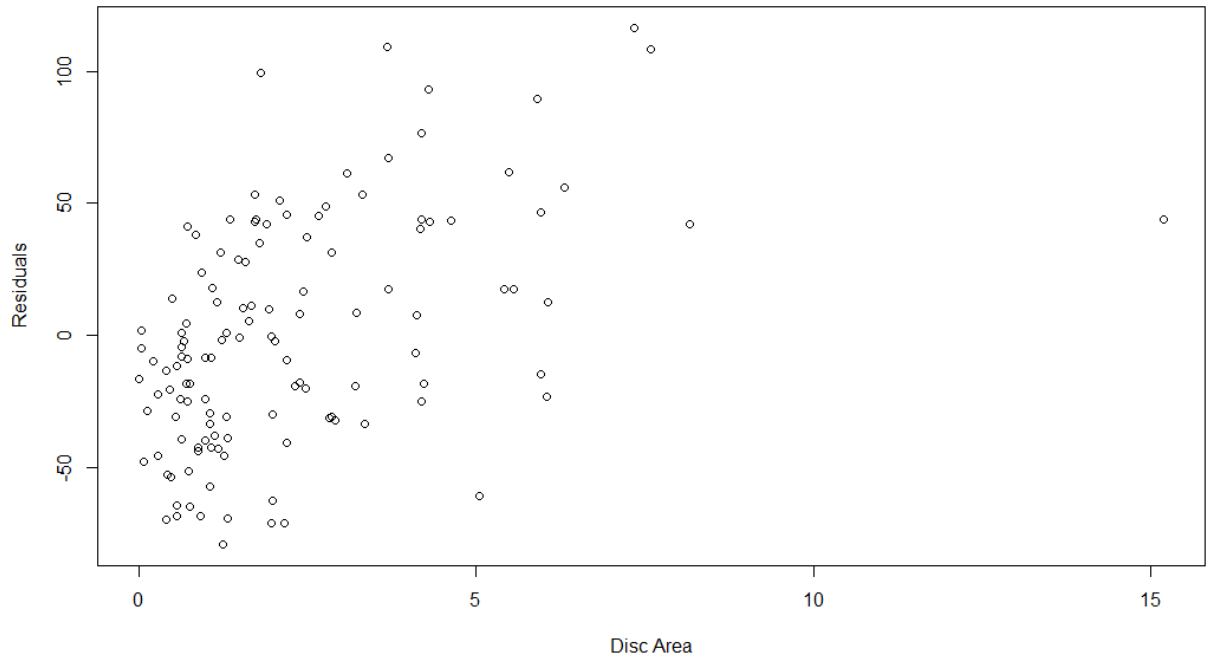


**Figure 8.** Comparison of mean distance between *P. barbatus* and *S. invicta* colonies at study sites with at least 8 *P. barbatus* colonies sampled. The dark bars represent  $X_{har}$  and the lighter bars represent  $X_{com}$ . None of the sites are different from the others ( $F_{7,80} = 0.29$ ,  $P = 0.96$ ). Error bars represent the 95% confidence intervals. See Figure 5 for study site locations.





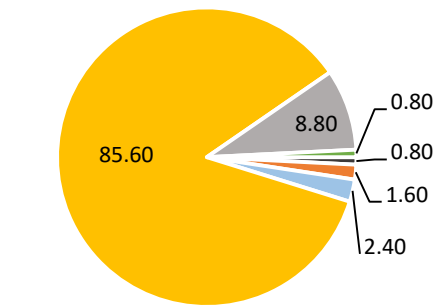
**Figure 9.** Comparison of fire ant density around *P. barbatus* colonies at study sites with at least 8 colonies sampled. The dark bars represent  $D_{har}$  and the lighter bars represent  $D_{com}$ . None of the sites are different from the others ( $F_{7,80} = 1.23$ ,  $P = 0.30$ ). Error bars represent the 95% confidence intervals. See Figure 5 for study site locations.



**Figure 10.** The relationship between disc area and the residuals from a simple linear regression of ant activity level vs. ground temperature. By using the residuals, the effect of ground temperature on ant activity level is accounted for prior to testing for a relationship between ant activity (residuals) and disc area. There is a significantly positive trend indicating that as disc size increases there are on average more ants in the colony ( $F_{1,123} = 36.6$ ,  $R^2 = 0.229$ ,  $P < 0.001$ ).

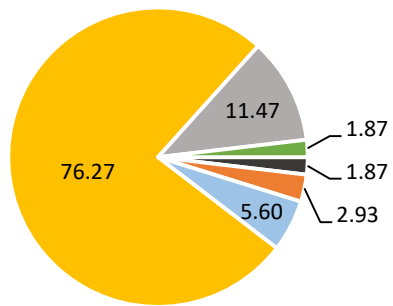


Focal *P. barbatus* colonies



■ Bare ■ Rock ■ Scrub  
■ Short Grass ■ Tall Grass ■ Trees

Comparison points



■ Bare ■ Rock ■ Scrub  
■ Short Grass ■ Tall Grass ■ Trees

**Figure 11.** Comparison of habitat types surrounding *P. barbatus* colonies and neighboring comparison points. The distribution of habitat types among the colonies (observed values) is not significantly different from the habitat types of the comparison points (expected values) ( $\chi^2 = 2.60$ ,  $P = 0.24$ ).

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