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EFFECTS OF HABITAT TYPE AND DISTANCE FROM EDGE ON ANT  
COMMUNITY COMPOSITION IN A DEGRADED NATURAL AREA

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**Abstract**

We examined the effects of habitat type and distance from the edge on ant species richness and community composition and we assessed the ability of species to dominate experimental bait stations in degraded longleaf pine savanna and oak hammock in northern Florida. We were particularly interested in the relationships between non-indigenous species, including *Solenopsis invicta*, and the native ant community. Species richness per pitfall trap was significantly higher in the pine habitat, but distance from the edge had no effect in either habitat. Although NMDS ordination showed substantial separation in community composition between the two habitat types, it also did not show any effect of distance from edge. Non-indigenous ant species, of which *S. invicta* was the most common, were significantly more abundant in the pine habitat. There was no relationship between the number of introduced and native species, but in the pine habitat the presence of *S. invicta* was significantly associated with lower richness of native ant species at small spatial scales. A small subset of the species dominated the bait stations, led by *S. invicta*. The results of the baiting study suggest that at least some non-indigenous species may persist in diverse ant communities due to their ability to find and dominate food resources.

**Key words:** ant sampling, edge effects, Formicidae, habitat heterogeneity, invasive species, non-indigenous species, *Solenopsis invicta*, species coexistence

**Introduction**

Ants (Hymenoptera: Formicidae) are diverse, abundant and important components of most tropical and temperate terrestrial systems (Hölldobler and Wilson 1990). The composition of ant communities may be influenced by interspecific competition (Davidson 1977, Andersen and Patel 1994, Gibb 2005), variation in resource availability and habitat quality (Palmer 2003, Boulton et al. 2005, Dauber et al. 2005), and temporal changes in activity (Herbers 1985, Bestelmeyer 2000, Albrecht and Gotelli 2001). Research in a wide variety of systems has shown that the short- and long-term effects of human activities affect ant communities of disturbed or developed areas (Abensperg-Traun et al. 1996, Bestelmeyer and Wiens 1996, Vasconcelos 1999). Because they are so sensitive to habitat variation and respond quickly to changes in habitat quality, ants may be excellent indicators of land management practices and restoration efforts (Majer 1996, Andersen et al. 2002, Andersen and Majer 2004, Ottonetti et al. 2006). Both habitat patch size and edge effects have been shown to affect the presence and relative abundance of ants in some systems (Punntila 1996, Abensperg-Traun and Smith 1999, Bolger et al. 2000, Gibb and Hochuli 2002, Braschler and Baur 2003, Bruhl et al. 2003, Dauber and Wolters 2004). However, it is important to note that the exact effects of anthropogenic habitat alteration vary among systems and among species within systems (Kotze and Samways 2001).

The state of Florida (USA), with 218 species, has exceptionally high ant diversity for the temperate zone (Deyrup 2003). This fauna includes at least 52 non-indigenous species (Deyrup et al. 2000), some of which are known to be highly competitive and have negative effects on populations of native ants and other arthropods (Porter and Savignano

1990, Suarez et al. 1998, Deyrup et al. 2000, Gotelli and Arnett 2000, Zettler et al. 2004).

At large scales the abundance of native and exotic species may be positively correlated due to external factors such as productivity and habitat heterogeneity (Morrison and Porter 2003, Davies et al. 2005, Harrison et al. 2006), but the strong competitive ability of the most successful invasive ant species often limits coexistence at small scales (Punntila et al. 1996, Morrison 2000). Because the invasion of non-indigenous species is often facilitated by anthropogenic disturbance, degraded areas often have depauperate native ant communities comprising many non-native species (Tschinkel 1988, Stiles and Jones 1998, Suarez et al. 1998, Zettler et al. 2004).

We studied the ant communities of oak hammock and longleaf pine savanna in a degraded natural area on the University of Florida's Gainesville campus. The site is small and highly fragmented, making it ideal for investigating the effects of small-scale habitat variation and the presence of invasive, non-indigenous ant species on overall ant community composition. We had three primary objectives in conducting this study: 1) to identify relationships between habitat type and community composition, 2) to determine the effects of distance from edge on ant community characteristics and 3) to assess the competitive ability of the most abundant ant species at the site using baits. In addressing these questions we were particularly interested in the how non-indigenous ant species, particularly the red imported fire ant (*Solenopsis invicta*), responded to habitat and edge effects and how their diversity compared with that of native species.

## **Methods**

### *Study site*

We conducted this study in the University of Florida's Natural Area Teaching Lab (NATL), a 24 ha site comprising a variety of upland and wetland habitats typical of northern peninsular Florida. We sampled ants in two small tracts of longleaf pine (*Pinus palustris*) that had been recently burned as part of an ongoing restoration project and an adjacent tract of oak hammock. There is evidence that single fires can alter the short-term community composition of ants (Izhaki et al. 2003) and that ant assemblages differ within a site according to time since fire (Lubertazzi 2003). All sites were grazed within the past 100 years and as recently as 40 years ago the two pine sites and one section of the hardwood sites were open-grown longleaf savannah. The study areas were separated by dirt roads that contrasted sharply with the bordering vegetation and provided habitat for a number of habitat generalist ants and open-ground specialists that were otherwise rare at the site (MDT, unpublished data).

#### *Collection methods*

We collected ants with pitfall traps and baits, methods that are complementary for generating robust species lists in the region (King and Porter 2005). Pitfall traps were 15 dram vials (approx. 3 cm diameter) partially filled with propylene glycol and left open for 48 hr. We arranged the pitfall traps in transects (6 traps per transect) running 15 m from the habitat edge perpendicularly into the study area. This allowed both a thorough sampling of the ant community at the site and an assessment of variation in community composition due to habitat preference or edge effects. We sampled two contiguous but distinct areas of the hardwood hammock and the two tracts of longleaf pine in late May and again in July 2005. For each sample period we placed 30 pitfall traps arranged in five transects in the two areas of each habitat type, totaling 240 pitfall traps for the study.

Bait stations were 15 dram vials within which we placed a small piece of Vienna sausage. We placed the vials on their sides and opened them for one hour, after which we capped the vials and then identified and counted all ants present at the bait in the lab. The sampling design was identical to that used for the pitfall traps but we used different transects and sampled only once in mid-June 2005 for a total of 120 bait stations.

#### *Data analysis*

The pitfall trap data were used to generate species lists to describe the ant community at the site, whereas the bait data were used primarily to demonstrate the competitive ability of individual species relative to their abundance. Because pitfall traps within transect were not independent samples, we used linear mixed-effects models that treated individual traps as repeated measures within transects to determine the effects of habitat type, sampling date and number of exotic species on species richness. We followed a standard protocol for linear mixed effects models (Pinheiro and Bates 2002) using maximum likelihood methods to fit model parameters. The two habitats were analyzed separately to test for potential interactions between native and introduced species because they differed substantially in the presence and abundance of non-indigenous species. Differences in community composition due to habitat preference, distance from edge and sampling date were assessed with non-metric multidimensional scaling (NMDS). We used logistic regression to determine the effects of sampling method on the capture probability for each of the five most abundant species (*Solenopsis invicta*, *S. carolinensis*, *Pheidole dentata*, *P. dentigula* and *P. moerens*). Only pitfall traps or bait stations that contained ants were included in this analysis. Data analysis was conducted with R v. 2.2.1 (R Development Core Team 2005). All species identifications

were made by the authors and voucher specimens have been deposited at the Florida State Collection of Arthropods (Florida Department of Agriculture, Division of Plant Industry, Gainesville, FL).

## Results

### *Pitfall traps*

In the pitfall traps we collected 2550 individual ants from 28 species, 7 of which are not native to Florida (Table 1). Abundance of species varied greatly, ranging from 882 individuals in 156 traps for *Solenopsis carolinensis* to one individual in one trap for *Aphaenogaster floridana*, *Eurhopalothrix floridana* and an unidentified *Pyramica*. Total species richness was higher in the longleaf pine habitat during both sampling periods (for both May and July: pine = 22 species, oak = 16 species). Date of sampling did not significantly affect species richness per trap, but there was significant variation between the two habitats (Likelihood Ratio = 17.47,  $P < 0.0001$ ). Species richness per trap was approximately 50% higher and more variable in the pine habitat (mean  $\pm$  SE =  $3.86 \pm 0.30$ ) than in the oak hammock (mean  $\pm$  SE =  $2.46 \pm 0.21$ ; Fig. 1). Although there was a marginally significant effect of distance from the edge on species richness per trap (Likelihood Ratio = 3.42,  $P = 0.064$ ), there was no clear pattern indicating a directional trend (Fig. 2). Maximum likelihood tests found no significant interaction between habitat type and distance from the edge on species richness per trap so it was not included in the final model. Community composition varied distinctly between habitats and between sampling periods (Fig. 3). However, there was no evidence that distance from the edge affected community composition in a consistent manner.

There was no significant difference between habitats in species richness per trap of native ants (Likelihood Ratio = 0.071,  $P = 0.79$ ). However, there were significantly more individuals of non-indigenous species per trap in the longleaf pine habitat (mean  $\pm$  SE =  $4.58 \pm 0.82$ ) than in the oak hammock (mean  $\pm$  SE =  $0.16 \pm 0.58$ ;  $F_{1,38} = 29.37$ ,  $P < 0.0001$ ). Distance to edge did not significantly improve model fit (Likelihood Ratio = 1.77,  $P = 0.18$ ), indicating that there was no edge effect on the number of individuals of non-indigenous species in this system (Fig. 4). Furthermore, the longleaf pine habitat had more non-indigenous ant species than the oak hammock both absolutely (pine = 6, oak = 2) and as a proportion of the total species richness (pine = 0.24, oak = 0.10). This important difference in response between native and non-indigenous species certainly contributed to the separation of the communities of the pine and oak habitats in the ordination plot (Fig. 3).

There was no overall effect of the number of non-indigenous ant species or the number of non-indigenous individuals on the number of native species per trap (Likelihood Ratio = 0.76,  $P = 0.38$  and Likelihood Ratio = 0.91,  $P = 0.34$ , respectively). Nor was there any effect of the number of introduced species on native species richness per trap when the two habitats were analyzed separately (Pine:  $t = 0.52$ ,  $df = 98$ ,  $P = 0.60$ ; Oak:  $t = 1.35$ ,  $df = 98$ ,  $P = 0.18$ ). In the pine habitat, the presence of *Solenopsis invicta* was not related to the number of individuals of native species but was significantly associated with lower native species richness at the trap level ( $t = 0.12$ ,  $df = 98$ ,  $P = 0.90$  and  $t = -2.11$ ,  $df = 98$ ,  $P = 0.037$ , respectively). In contrast, in the oak habitat, the presence of *Solenopsis invicta* was not related to either the number of individuals or



richness of native species per trap ( $t = -0.70$ ,  $df = 96$ ,  $P = 0.48$  and  $t = 0.41$ ,  $df = 96$ ,  $P = 0.68$ ).

### *Bait stations*

There were 14 species present at the baits, totaling 5535 individuals (Table 2). One species at the bait stations, *Monomorium viride*, was not collected in the pitfall traps. Of the 117 bait stations recovered, 88 contained ants and only a single ant species was present at approximately three-quarters ( $n = 65$ ) of these baits. *Solenopsis invicta*, *S. carolinensis* and *Pheidole moerens* dominated the most baits (19, 18 and 9, respectively). Logistic regression showed that the probability of capture of *S. invicta* did not differ between pitfall traps and baits, although there was a non-significant positive effect of the bait method on capture probability and the mean number of individuals per sample was much higher for bait stations. The three most abundant native species, *Solenopsis carolinensis*, *P. dentata* and *P. dentigula*, were all significantly less likely to be captured at the bait stations compared to the pitfall traps ( $p < 0.001$  for all three species). The capture probability for *P. moerens* was also lower with the baits ( $p < 0.001$ ), but this species was significantly more likely to be captured at the bait stations than in the pitfall traps in the oak hammock ( $p < 0.001$ ).

## **Discussion**

Habitat and resource partitioning in ant communities is determined by both environmental factors and interactions among potentially coexisting species (Hölldobler and Wilson 1990, Albrecht and Gotelli 2001). We did not analyze the habitat preferences of individual species, but there was clear separation between the ant communities of the

two habitat types and the affinity of species for either the oak hammock or degraded longleaf pine savannah is evident in Table 1. Additionally, we found more species in the pine habitat overall and significantly more species per pitfall trap in the longleaf pine tracts than in the oak hammock. Some species showed predictable patterns of abundance, such as the open habitat specialist *Dorymyrmex bureni*, but the occurrence of other species was more enigmatic, such as the higher abundance of the litter-dwelling *Pyramica* and *Strumigenys* species in the recently burned pine habitat than in the oak hammock. Although there is some evidence that ant communities change with distance from habitat edge (Bolger et al. 2000, Dauber and Wolters 2004, Ness 2004), we detected no significant edge effects on species richness or community composition. It is possible that we failed to capture the edge effect; alternatively, it is possible that the degradation of the habitat renders even interior portions as functionally marginal habitat for ants.

Our analyses failed to show any correlation between introduced species as a whole and the number of native species present at the trap level. However, it appeared that the higher species richness in the longleaf pine tracts at both the trap and habitat level was entirely attributable to the presence of more non-indigenous species. Previous research has shown that disturbance can increase the abundance of many introduced ant species sometimes with consequent negative effects on the native ant community (Suarez et al. 1998, Bolger et al. 2000, Andersen and Majer 2004). Both the oak hammock and the longleaf pine area have been substantially degraded, but the longleaf pine habitat currently experiences more frequent and severe disturbances (e.g., fire, woody vegetation removal and soil perturbation from planting pines and wiregrass) as part of ongoing ecological restoration work. It remains a possibility that some native species have been

displaced in these sites due to competition with introduced species, but our study was not designed to test this hypothesis directly.

The red imported fire ant, *Solenopsis invicta*, was rare in the oak hammock (13 individuals in 4 pitfall traps), but was among the most abundant species in the longleaf pine savanna (279 individuals in 70 pitfall traps). This species was also the most abundant ant at baits, both in number of individuals and number of baits dominated. The presence of *S. invicta* can reduce native ant diversity at both small (Porter and Savignano 1990, Morris and Steigman 1993) and large spatial scales (Gotelli and Arnett 2000). However, there is also evidence suggesting that the initial effects of fire ant invasion may eventually relax and that other habitat factors may promote both native ant diversity and fire ant abundance (Morrison 2002, Morrison and Porter 2003). We found that the presence of *S. invicta* was negatively associated with native ant species richness at the trap level in the longleaf pine savanna but not in the oak hammock or when data from both habitats were pooled. This suggests that at very small scales (i.e., the trap level), *S. invicta* outcompeted or reduced the species density of native ants, and perhaps other non-indigenous ant species as well. Such a finding is consistent with the widely-recognized ability of *S. invicta* to dominate resources and exclude other species (Deyrup et al. 2000, Morrison 2000) and is consistent with our data from the baiting study. Because *S. invicta* is abundant in both disturbed areas and frequently-burned longleaf pine savannas (Tschinkel 1988, Lubertazzi 2003, Zettler et al. 2004)) this species will likely persist at the site with unknown consequences for other ant species.

The ants captured at the bait stations included a smaller proportion of non-indigenous species than those captured with pitfall traps (14.3% and 25%, respectively).

However, these two species, *S. invicta* and *P. moerens* were among the three most dominant species at the baits and *S. invicta* was the only one of the five most abundant species overall that was not less likely to be captured with baiting. Similarly, although *P. moerens* was relatively rarely captured in the oak hammock with pitfall traps, it was the second most frequently captured species at the bait stations in that habitat. This finding suggests that these two species are dominant at the NATL site both numerically and competitively. The dominance of *S. invicta* in disturbed habitats in the southeastern US is widely recognized, and *P. moerens* has been identified as a potential threat to native ants or other arthropods in Florida (Deyrup et al. 2000). Our study confirms the former finding and indicates that the latter suggestion may merit further study.

In summary, we found strong support for the division of two distinct ant communities associated with different habitats in a degraded natural area in northern Florida but no effect of distance from the edge on community composition or species richness. Non-indigenous species were abundant in the longleaf pine habitat but relatively rare in the oak hammock, perhaps due to differences in site history and current disturbance regime associated with ecological restoration efforts. We found some evidence of competitive exclusion by imported red fire ants at the trap level in the pine habitat, but no effect of *S. invicta* presence or abundance on native ants at larger scales. Although our study was conducted at a single site, the NATL is perhaps representative of many small, fragmented and degraded parks and natural areas in the region.

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Table 1. Summarized data for the 28 species collected in pitfall traps, noting the number of individuals and the number of traps for each species, divided by habitat.

<u>Species</u>	<b>Habitat</b>			
	<b>Oak hammock</b>		<b>Longleaf pine</b>	
	<u>Individuals</u>	<u>No. traps</u>	<u>Individuals</u>	<u>No. traps</u>
<i>Aphaenogaster ashmeadi</i>	3	3	14	10
<i>Aphaenogaster carolinensis</i>	7	7	0	0
<i>Aphaenogaster floridana</i>	1	1	0	0
<i>Brachymyrmex depilis</i>	3	3	7	4
<i>Brachymyrmex musculus</i>	0	0	40	13
<i>Camponotus castaneus</i>	27	19	11	9
<i>Camponotus floridanus</i>	22	20	8	5
<i>Cardiocondyla emeryi</i>	0	0	38	18
<i>Crematogaster ashmeadi</i>	1	1	1	1
<i>Cyphomyrmex rimosus</i>	0	0	23	15
<i>Dorymyrmex bureni</i>	0	0	56	14
<i>Eurhopalothrix floridana</i>	1	1	0	0
<i>Formica pallidefulva</i>	16	12	82	35
<i>Hypoponera opacior</i>	8	6	15	13
<i>Odontomachus brunneus</i>	47	37	31	23
<i>Pheidole dentata</i>	199	77	136	34
<i>Pheidole dentigula</i>	167	69	108	41
<i>Pheidole metallescens</i>	3	1	78	18
<i>Pheidole moerens</i>	6	4	188	38
<i>Pyramica eggersi</i>	0	0	8	6
<i>Pyramica membranifera</i>	0	0	8	2
<i>Pyramica sp.</i>	0	0	1	1
<i>Solenopsis carolinensis</i>	435	75	447	81
<i>Solenopsis invicta</i>	13	4	279	70
<i>Solenopsis nickersoni</i>	1	1	1	1
<i>Solenopsis tennesseensis</i>	1	1	3	3
<i>Strumigenys louisianae</i>	0	0	2	2
<i>Trachymyrmex septentrionalis</i>	2	2	2	2

Table 2. Summarized data for the 14 species collected at the bait stations, noting the number of individuals and the number of traps for each species, divided by habitat.

<u>Species</u>	<b>Habitat</b>			
	<b>Oak hammock</b>		<b>Longleaf pine</b>	
	<u>Individuals</u>	<u>No. traps</u>	<u>Individuals</u>	<u>No. traps</u>
<i>Aphaenogaster ashmeadi</i>	11	3	0	0
<i>Aphaenogaster carolinensis</i>	33	3	0	0
<i>Camponotus floridanus</i>	17	4	6	1
<i>Cardiocondyla emeryi</i>	0	0	1	1
<i>Formica pallidefulva</i>	3	3	19	1
<i>Monomorium viride</i>	0	0	1	1
<i>Odontomachus brunneus</i>	10	4	1	1
<i>Paratrechina faisonensis</i>	5	3	1	1
<i>Pheidole dentata</i>	19	5	89	6
<i>Pheidole dentigula</i>	24	4	0	0
<i>Pheidole metallescens</i>	61	1	0	0
<i>Pheidole moerens</i>	457	11	168	8
<i>Solenopsis carolinensis</i>	376	14	249	11
<i>Solenopsis invicta</i>	16	2	3968	26

**Figure legends**

Figure 1. Species richness per trap was significantly higher in the longleaf pine savanna than in the oak hammock. Boxplots show median (**bold**), minimum, maximum and interquartile range.

Figure 2. Species richness per trap was marginally significantly affected by distance from edge, but there was no clear directional trend. Boxplots show median (**bold**), minimum, maximum and interquartile range of all traps at each distance.

Figure 3. NMDS ordination plot of ant community composition. Traps in each habitat for each date were pooled according to distance from edge, and are labeled as such (1 = 1 m, 2 = 4 m, 3 = 7 m, etc.). There are clear differences between the two habitat types and the two sampling dates, but no apparent pattern in community composition related to distance from edge.

Figure 4. Number of individuals of all non-indigenous species per trap was significantly higher in the longleaf pine habitat but was not affected by distance from edge.

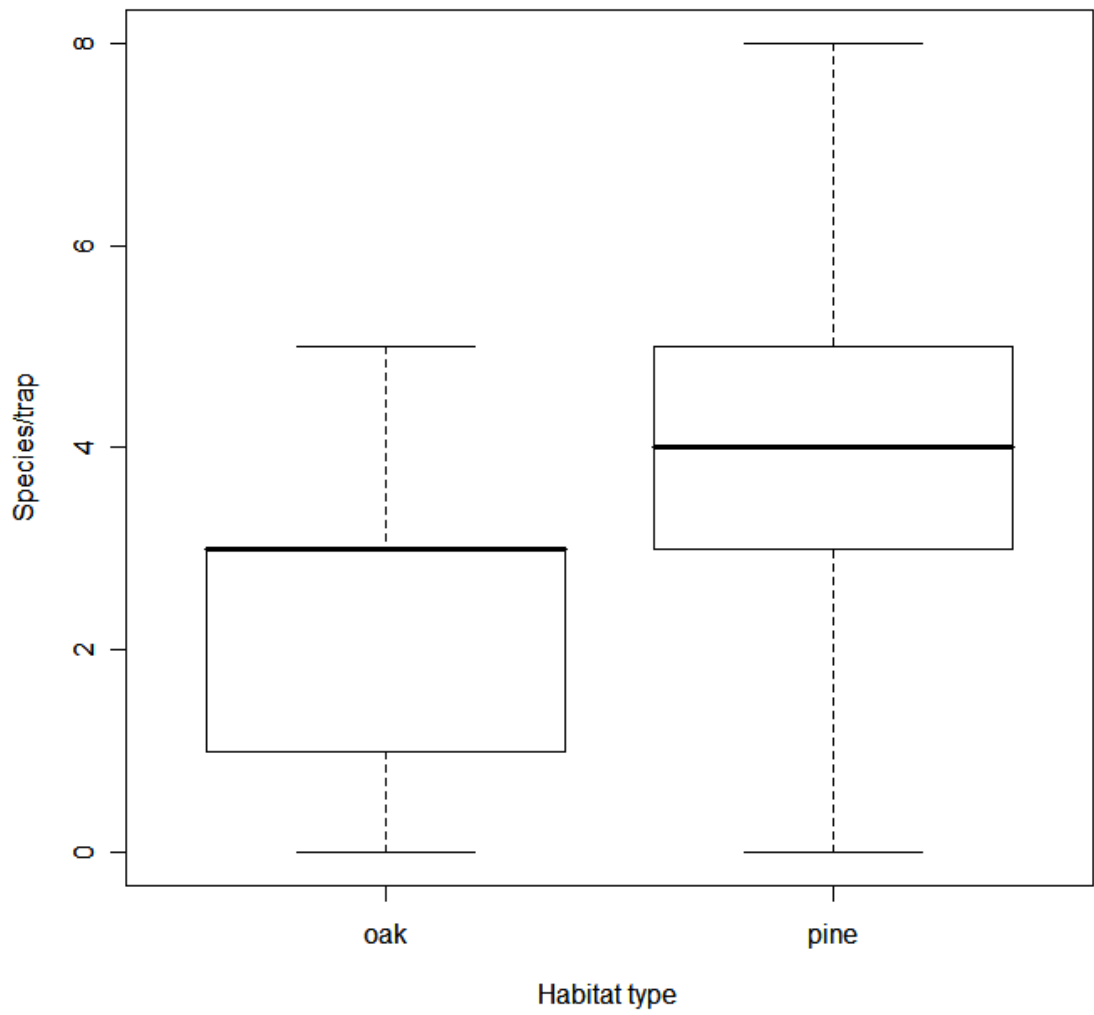


Fig. 1

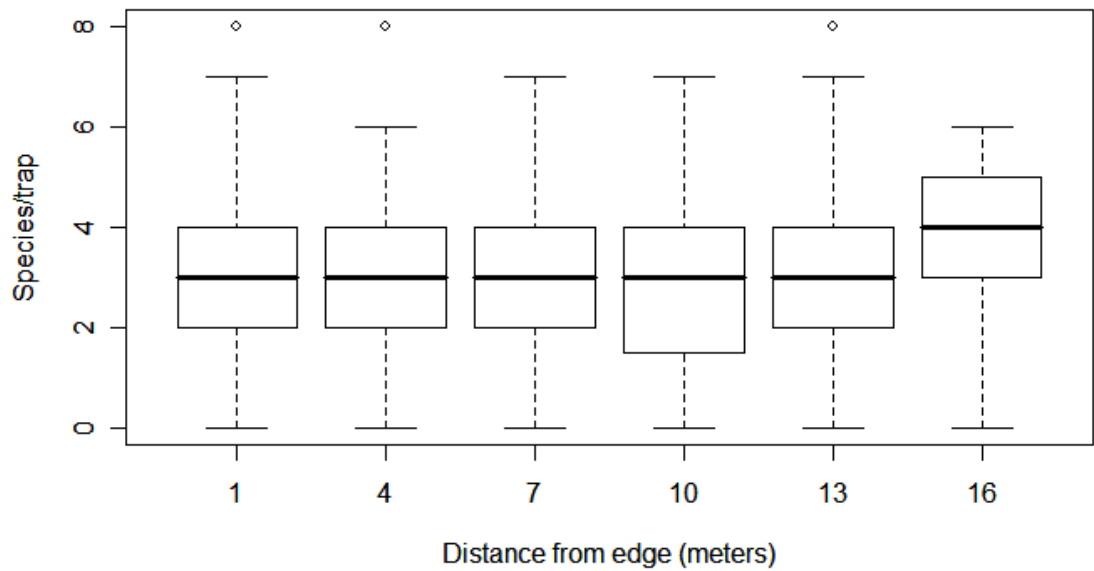


Fig. 2

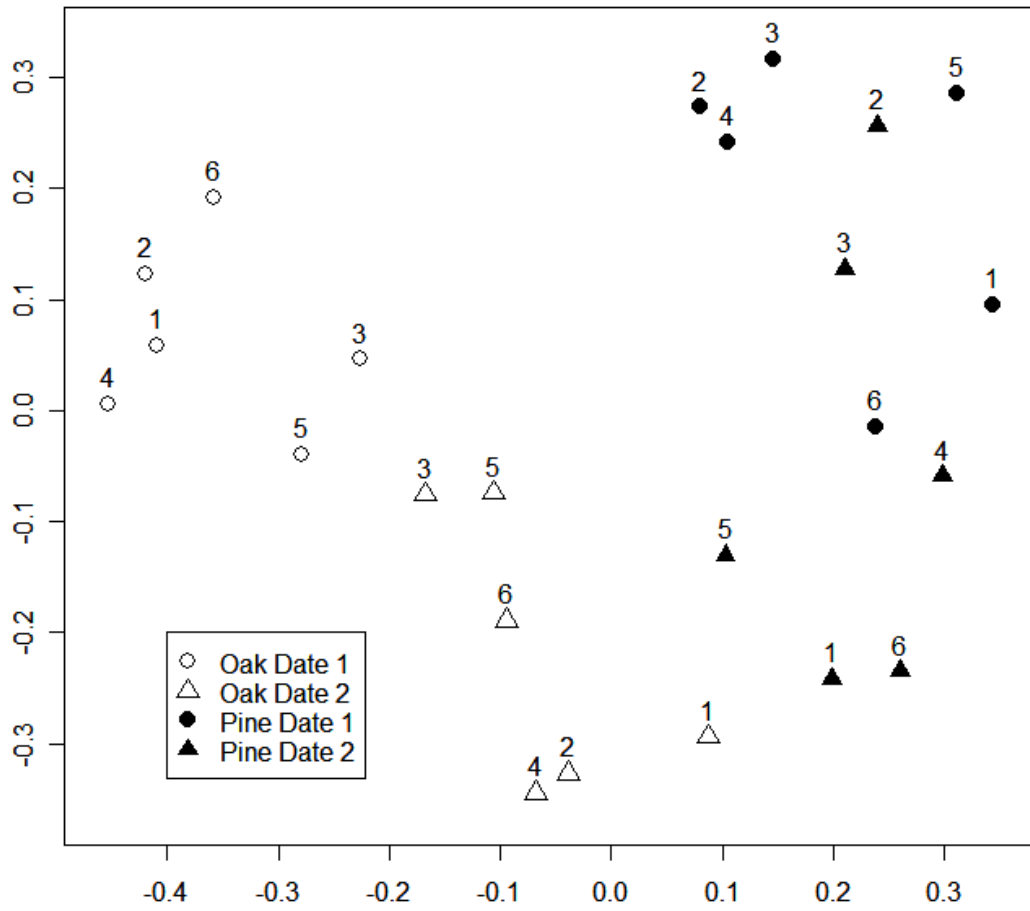


Fig. 3



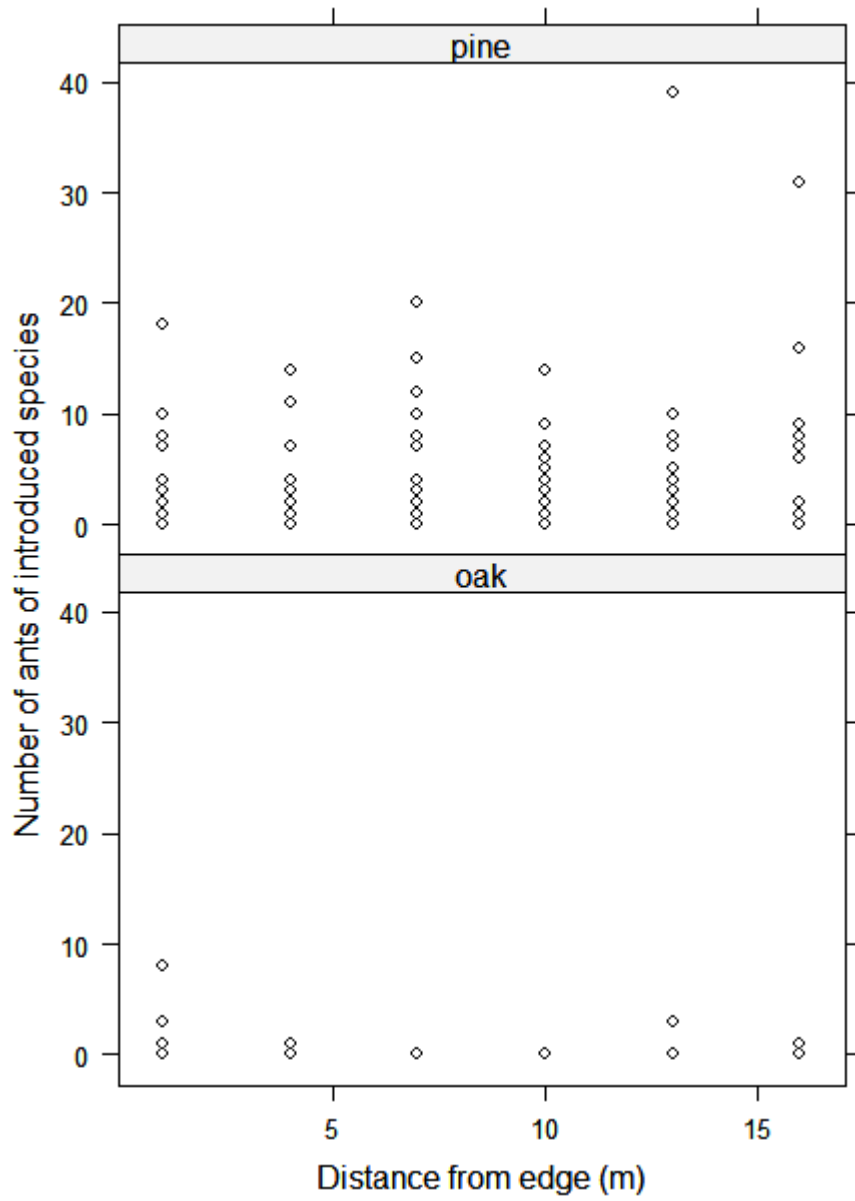


Fig. 4