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Ant community change across a ground vegetation gradient in north Florida's longleaf pine flatwoods

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Abstract

Ant communities in longleaf pine habitats are poorly known and hence the naturally occurring ant assemblages of a large portion of southeastern North America are not well understood. This study examined the diverse ant community found in the longleaf pine flatwoods of north Florida and tested how ant diversity changes along a herbaceous ground cover gradient. Restoring the ground cover to its original floral composition is an important focus of longleaf pine conservation and hence it is important to understand how native faunal communities vary with ground cover variation. Using 4 sampling methods, we characterized the ant community and analyzed its within-habitat variation among 12 study sites. We found the highest plot species richness (55 species) and within-habitat species richness (72 species) ever recorded for North American ants. The ants formed three distinct communities. The low-diversity arboreal and subterranean assemblages varied little across forest stands while the diversity of the species-rich ground foraging ant community was negatively correlated with percent herbaceous cover. The imported fire ant, *Solenopsis invicta* (monogyne form), was unexpectedly found to be abundant in high herbaceous cover sites. Floral restoration of the pine flatwoods, which is increasing the proportion of herbaceous cover, is likely to cause an increase in the abundance of the imported fire ant.

Keywords: Formicidae, *Pinus palustris*, *Solenopsis invicta*, conservation biology, ant community

Abbreviation:

ANF Apalachicola National Forest

Introduction

Community level studies of ants in longleaf pine (*Pinus palustris*) habitats have investigated subsets of the overall ant community (Tschinkel 1988; Prather 1997; Tschinkel and Hess 1999) or produced checklists of species found in a particular area (Van Pelt 1956; Deyrup and Trager 1986; Campbell 1996). Little work has been done to examine the entire ant community across numerous sites in any specific longleaf pine habitat. We therefore know little about the ant communities that, until recently, occurred naturally throughout a large part of the southeastern United States.

Learning more about longleaf pine ant communities is important not only to further our understanding of North American ants but also to guide current longleaf pine conservation efforts. Before Europeans arrived in North America longleaf pine covered over 30 million hectares and dominated the Atlantic and Gulf coastal plains. Today longleaf pine is found in less than 3% of its historical range (Frost, 1993) and what does remain forms some of North America's most threatened habitats (Noss 1989; Simberloff 1993; Collins 2001). While the floral diversity found in some longleaf

pine habitats is among the highest known for any temperate zone plant communities (Peet and Allard 1993), studies of faunal communities in these habitats are rare (reviews in Hermann 1993; Stout and Marion 1993). Animal research has focused on a few threatened or economically important species such as *Picoides borealis* (red cockaded woodpecker, Walters 1991), *Gopherus polyphemus* (gopher tortoise, Aresco and Guyer 1999) and *Colinus virginianus* (bobwhite quail, Rosene 1969). Effective preservation of remnant longleaf pine forests demands more research to catalog resident species, to understand species associations, and to identify organisms that need special attention because of their rarity or endemism. Carefully planned community studies can efficiently fill some of these needs and add to our general knowledge of these habitats.

Studying the ant community can also help us understand an important component of longleaf pine ecosystems. Social insects often constitute more than half of all the insect biomass in many terrestrial habitats (Wilson 1990) and ants in particular are one of the most well represented groups (Hölldobler and Wilson 1990; Tobin 1995; Longino and Colwell 1997). A large body of literature

documenting the various ecological roles ants fill in terrestrial ecosystems (Beattie 1985; Wilson 1990; Gotwald 1995) highlights the important direct and indirect effects ants can have on many organisms. Within longleaf pine habitats ants are likely to interact with many resident species and affect populations of a diverse collection of flora and fauna.

One important role filled by ants in a longleaf pine ecosystem has already been found. Hess and James (1998) discovered that the arboreal ant *Crematogaster ashmeadi* is the dominant food item in the diet of the adult endangered Red Cockaded Woodpeckers of the Apalachicola National Forest (ANF). This finding has stimulated research investigating *C. ashmeadi*'s autecology (Hahn and Tschinkel 1997; Baldacci and Tschinkel 1999; Tschinkel 2002) and the arboreal ant community of the ANF's pine forests (Prather 1997; Hess and James 1998; Tschinkel and Hess 1999). The more diverse ant community found beneath the trees has not been studied.

Our research examined the complete ant community found in the ANF's pine flatwoods. We sampled ants, using four methods,

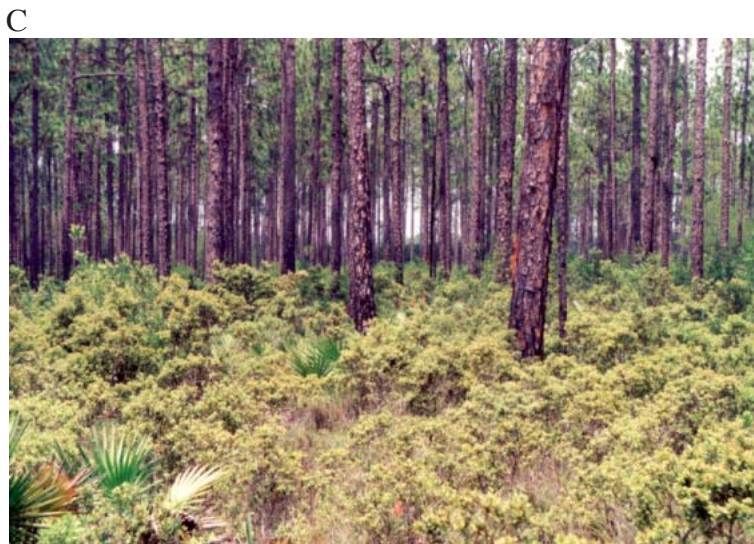
in twelve sites. The aims of our work were to establish the species composition of the longleaf pine flatwoods ant community, to determine its dominant species, and to assess how ant diversity changes along a herbaceous ground cover gradient. We specifically focused on examining the ant community across this gradient because this habitat characteristic is an important focus of contemporary longleaf pine conservation.

Materials and Methods

Study Area/Study sites

The ANF lies in the Big Bend region of Florida and contains over 50,000 ha of longleaf pine forest. Pine flatwoods (Abrahamson and Hartnett 1992), our focal study habitat, develop on slightly undulating, sandy plains with a high water table, and are common here (Fig 1). Under natural conditions, these stands once contained widely spaced old growth longleaf pine trees (Platt et al. 1988) and a grass-dominated ground cover. Contemporary longleaf pine forests, in contrast, are almost exclusively second growth stands,

Figure 1. Pine flatwoods of the Apalachicola National Forest. (A & B). Stands with a high percentage of herbaceous vegetation. (C & D). Stands with a woody plant dominated ground cover.



are more densely stocked, and contain populations of younger, smaller trees (Noel et al. 1998). Anthropogenic changes to the natural fire regime have also decreased the dominance of herbaceous plant cover in many ANF longleaf pine stands (James et al. 1997, U.S. Department of Agriculture 1999a).

Current ANF management plans call for restoring and maintaining longleaf pine stands in a state that “falls within the natural variation of this habitat type” (U.S. Department of Agriculture 1999b). To this end, the Forest Service has decreased logging to increase the average tree age and size. Restoring the ground cover, and maintaining it in a more natural state, is being attempted through the use of prescribed fire. The natural fire regime once suppressed the growth and establishment of understory woody plants, stimulated herbaceous plant growth and reproduction, and did little harm to mature longleaf pine trees. The Forest Service is mimicking this process by trying to burn the ground vegetation, during the growing season, every three years (Ferguson 1998, U.S. Department of Agriculture 1999a). It is not known how this management will affect resident animal communities.

The twelve study sites we sampled from were chosen from a larger pool of 24 pine flatwood stands. Prior sampling, for an unrelated study (James et al. 1997), allowed us to classify these stands into low, medium, or high grassy cover and we randomly selected four sites from each of these classes. Seven of our study sites, and all four sites with high herbaceous cover, were located in the Apalachicola Ranger District. Of the two management districts in the ANF, the Apalachicola Ranger District historically experienced more cattle grazing and prescribed fires than the Wakulla Ranger District. Apalachicola Ranger District pine flatwoods also contain, in general, a higher percentage of wiregrass (*Aristida stricta*) in their ground cover. None of our high herbaceous study sites were located in the Wakulla Ranger District because we had no prior surveyed stands from this area in this class. Distances between our study sites ranged from 4 to 55 km.

Ant sampling

Pitfall trapping, ground baiting, subterranean baiting, and tree baiting were used to sample the ant community. These methods were used together in order to comprehensively sample ants above, below, and at the ground surface. At each site a 70 m x 80 m plot was established and subdivided into fifty-six 10m x 10m squares (Fig. 2). The corners of these squares were marked with flagging, forming a grid with 72 evenly spaced sample points (hereafter referred to as bait stations). These plots were sampled in June and July of 1998.

Pitfall trapping. Pitfall traps were positioned in the center of each of the 56 squares within a sample plot and left for six days. The traps were made from plastic Solo® (www.solocup.com) drink cups (0.27 L volume, 8.8 cm diameter at cup lip), buried so that the lip of the cup was placed flush with the ground surface, and partially filled with an ethylene glycol and water mixture. A 22.8 cm styrofoam plate was suspended over each trap to prevent rain from falling directly into the cups. This protocol was developed from prior test sampling (Lubertazzi, unpublished data) where collection curves for a variety of pitfall trap sizes, number of traps, and trapping duration were compared to establish a design that would capture most of the ant diversity within a site. Ants captured in pitfall traps

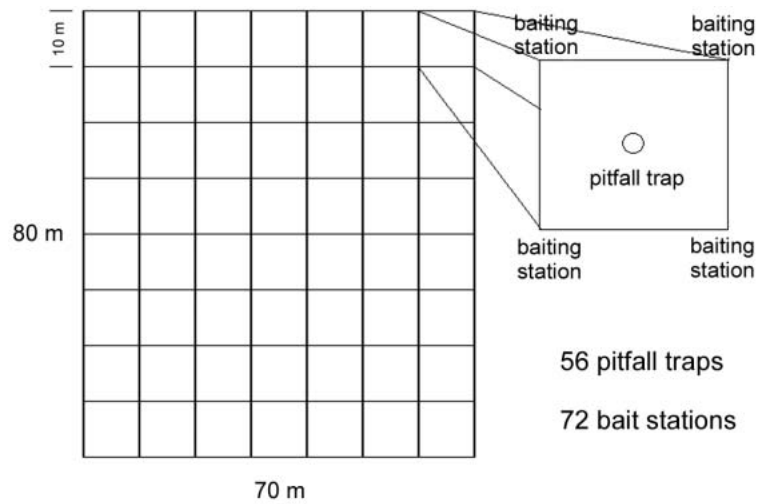


Figure 2. Sampling grid design used to sample the ant community within each plot.

were sorted from the cups in the lab, identified to species, and their abundance recorded.

Ground baiting. Ground foraging ants were sampled by placing baited tubes at each bait station within a plot. Baits consisted of 1 cm x 9 cm glass tubes containing a small portion of Spam®, a protein rich food source readily consumed by most omnivorous ants. Bait tubes were placed within 5 cm of a bait station with the lip of the tube touching the ground, and collected after ~ 30 minutes. Ant species that were both readily identifiable and easily quantified were immediately recorded as occupying such baits, others were collected and brought to the lab to be counted and identified.

Maximum ant foraging diversity in the ANF's pine flatwoods was found from 23° C - 29.5° C but even at these temperatures, foraging activity may be curtailed by a recent soaking rain (Lubertazzi, unpublished data). Collecting conditions were therefore standardized by sampling each plot in the mid morning when the temperature was ~ 28° C and only on sunny days when no heavy rain had fallen during the previous 12 hours.

Tree baiting. Every tree > 2 m tall within a plot was baited using one cm diameter filter paper disks dipped in a blended cat food/water/oil mixture (2:1:0.25). These baits were placed on a tree, at each of the four cardinal directions, 2 m from the ground. After approximately 30 minutes the abundance of each ant species at each bait was recorded. This protocol was slightly modified from that of Tschinkel and Hess (1999).

Tree baiting was carried out in the late morning and early afternoon. The temperature at this time of day does not appear to influence arboreal ant activity (Tschinkel and Lubertazzi, unpublished data) but ground-nesting species that may forage on the trees could be less active during this warmest part of the day.

Subterranean baiting. Subterranean ant species were sampled at each bait station using buried baits. This sampling was initiated at least one day after the ground baiting at each plot; buried baits were left for two days. Two-ml polypropylene cryogenic vials, with their sides perforated using a heated wire, were used as bait tubes (MacKay and Vinson 1989). These vials were filled halfway with Spam® and buried to a depth of 10 cm. A wire attached to each vial, and extending to the soil surface, was used to pull the bait

tubes from the ground. Each vial was quickly placed in its own container once it was pulled from the ground, preventing ants from escaping. Ants were sorted, counted, and identified to species in the lab.

Environmental variables

Aristida stricta (wiregrass), *Serenoa repens* (saw palmetto), *Ilex coriacea* and *I. glabra* (gallberry), *Quercus minima*, and *Q. pumila* (runner oak) are common ground cover plants in ANF longleaf pine stands. Within any site one, or at most a few, of these species generally constitute most of the ground cover biomass. We sampled the ground vegetation within each plot by placing a 1-m² quadrat at each bait station and visually estimating the percent cover of these common plants. The percent cover of other plant species, classed as other-herbaceous or other-woody vegetation, the percent exposed ground, and a ground litter score (sparse, light, medium or heavy) was also noted for each sample quadrat. To quantify the forest stand the diameter at breast height of all longleaf pines within each plot was measured and recorded.

Analysis

Ant species richness was compared among sites by using the total number of species observed within a site and by rarefying the pitfall trap data. Rarefaction can provide estimates, through interpolation, of the expected number of species found in a random sub-sample from a larger pool of samples (Simberloff 1979). Site species richness, as determined from pitfall data, could thereby be compared on an equivalent basis among sites without the problems associated with unequal sample sizes. We choose to not use baiting data in this analysis because the clumped occurrences of ants recruited to baits may bias rarefaction estimates (Simberloff 1979; Gotelli and Graves 1996; Collins 1998). The evenness of the ant community was compared among sites through the use of log abundance-rank plots (May 1975) and by using the rarefaction curves generated from the pitfall trap data.

The subterranean baiting, tree baiting, and pitfall trap data sets were examined with correspondence analysis to determine how each site's ant community was similar, or different, from other sites. Correspondence analysis is an exploratory data analysis method that can reveal such patterns through ordinating site-by-species contingency table data (Greenacre and Verba 1984; Zorrilla et al. 1986; James and McCulloch 1990). Each site is reduced to a plotted point that is positioned in an ordination graph according to its species composition and each species' abundance. Differences between sites are shown through the relative distance and direction between each site's ordinated position. In our analysis, points positioned close to one another represent sites having similar ant communities.

Ground baiting samples were used to identify the dominant ground-foraging species. In order to better categorize these data according to what we know about the biology of ant foraging behavior, and the ability of particular ant species to numerically and behaviorally dominate other ants, the number of workers of the particular species found at each bait sample were converted to an abundance score (1, 1 ant; 2, 2-5 ants; 3, 6-20 ants; 4, 21-50 ants; 5, 51-100 ants; and 6, >100 ants). A species with consistently low abundance scores (1-2) at baits is likely to forage singly and/or not recruit well to food finds. Intermediate scores (3-4) are indicative

of species that can recruit to food but are not overwhelmingly numerically or behaviorally dominant. Species with consistently high scores (5-6) are potentially important competitors that could deny other ants access to resources such as food and nesting sites. Our categories make it easier to not only differentiate species along this continuum of increasing dominance but also make it simpler to differentiate species within these groupings – especially for those species that are dominant. The more a species dominates food finds, the greater the range and variability in the number of workers that may be found at a bait and the less useful raw worker numbers are for deriving useful comparative statistics.

We calculated the average abundance score for each species within a site by taking the sum of a species' abundance scores for that site divided by the number of baits it occupied. An ant species found with 3, 10, 149, and 242 workers (101 mean workers per bait and an average abundance score of 4) is easily shown to be less dominant than a species with 101 workers at each of four baits (average abundance score of 6). The proportional site abundance score, calculated as a species' average site abundance score multiplied by the proportion of all ant-occupied baits a species was found at within that site, was used to compare the dominance of species within a site. Greater relative dominance is indicated by a higher score and species that increasingly dominate a site (evidenced by increasingly disparate average abundance scores and by occupying more of the baits at a site) show a relatively larger difference between their score and scores of other species.

Results

Ant diversity

A total of 72 ant species (Appendix A), representing 25 genera and 5 subfamilies, were found among the nearly 110,000 ants sampled. Total site species richness, found by combining the species data for all the sampling methods for each site, ranged from 31 to 55 species (Fig. 3). The pitfall traps yielded 25 - 46 species per site (Fig. 3, Appendix B) with non-pitfall trap samples adding an additional 3 - 9 species per site. Species richness estimates of the pitfall trap data, rarefied to 1250 individuals (the lowest total ant abundance in pitfalls in any site was 1263 individual ants), gives a site species richness range of 23-39 species (Fig. 3). The rarefied pitfall trap species richness, total pitfall trap species richness, and total site species richness all show close agreement in how they order the sites from low to high species richness.

The ground foraging ant community sampled by the pitfall traps is most even in sites 231 and 336. The initial steep rise of their rarefaction curves shows these sites accumulate species at a faster rate, compared to all other sites, as additional ants are sampled (Fig. 4). This contrasts with the shallow rarefaction curves of sites 79, 322 and 73, plots that exhibited the lowest evenness. Log abundance-rank plots (Fig 5) showed similar results. The ant assemblages found in the subterranean and arboreal zones (see results below) are not even. Each of these areas is numerically dominated by a single ant species.

Eight of the 72 ant species (11%) we found are not native to Florida (Deyrup, Davis, and Cover 2000). *Solenopsis invicta* (monogyne form), *Cardiocondyla wroughtonii* and *Cyphomyrmex rimosus* were found in many plots, *Brachymyrmex musculus* and

Pheidole moerens were locally abundant in a few plots and *Paratrechina vividula*, *Pyramica margaritae* and *Pyramica membranifera* were very rarely found.

Environmental variation

Vegetation sampling. The sites varied greatly in the proportions of their dominant ground cover plants (Table 1). *A. stricta* was abundant in areas containing a high percentage of herbaceous cover and *Quercus* species were common in areas dominated by woody plants. Reducing the vegetation data to herbaceous and non-herbaceous classes (Table 1) shows that our study plots sampled the full range of the herbaceous ground cover gradient. Sites varied from 2.4% to 89% herbaceous cover.

Other stand attributes. The number of trees found within each plot and the mean diameter at breast height (DBH) of the trees within these stands varied among sites (Table 2c). Site 79 had the fewest trees (53) and the largest average DBH (35.6 cm). The greatest number of trees was found in site 101 (282) and the lowest mean DBH was recorded in site 322 (19.1 cm). While all of these stands are considered mature forest, variation is found among sites in their tree demographics.

Average ground-litter ranks (sparse = 1, light = 2, medium = 3, and heavy = 4) were also variable (Table 1). Nine sites had an average litter rank score between 1.6 and 2.0. Site 79 had the lowest litter score at 1.1 while the highest litter scores were 2.5 for site 208 and 2.4 for site 3. Percent exposed ground varied from 9% in site 77 to 33% in site 208 (Table 1).

Ant sampling

Pitfall traps. Excluding gynes, 29,065 individual ants from 70 species were captured in 664 pitfall traps (Table 2a, Appendix B). Thirteen traps were lost during sampling. Ordination of the pitfall

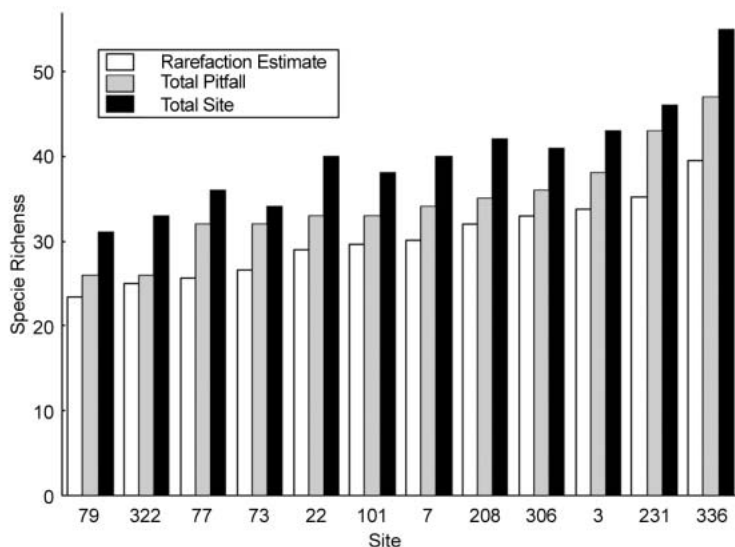


Figure 3. Species richness, by site, using three different richness values: rarefaction estimate of each site's pitfall trap samples standardized at 1250 individuals, uncorrected species richness for the pitfall trap data, and total site species richness combining all sampling methods. The sites are ordered along the abscissa from low to high species richness using the rarefaction estimate of species richness.

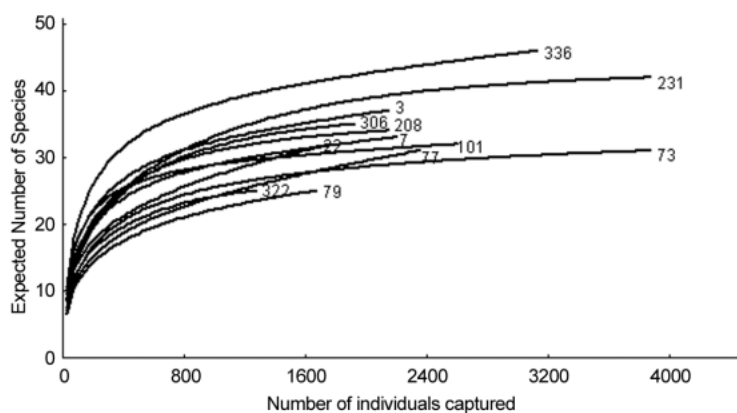


Figure 4. Rarefaction curves, by site, for ants captured in pitfall traps.

trap data (Fig. 6) shows five sites (3, 7, 101, 208, and 322) grouped in a loose cluster slightly above and to the left of the centroid (the 0, 0 coordinate). Five other sites were arranged progressively further to the right of this cluster by their increasingly higher dimension 1 values, and a few sites were found toward the lower left corner of the ordination. The patterning of sites along the second dimension forms an arc, indicating correspondence analysis is not deriving a second dimension solution that is orthogonal to the variation captured in the first dimension (ter Brakk 1996). This problem does not influence the quality of the first dimension result and the interpretation of these data will focus on the positioning of sites along this single dimension.

Coding sites by their percentage herbaceous ground cover (Fig. 6) shows ant community change, moving from left to right along the first dimension, parallels an increase in the percentage of herbaceous ground cover found within a site. Dimension 1 site scores show a strong positive correlation with percent herbaceous cover

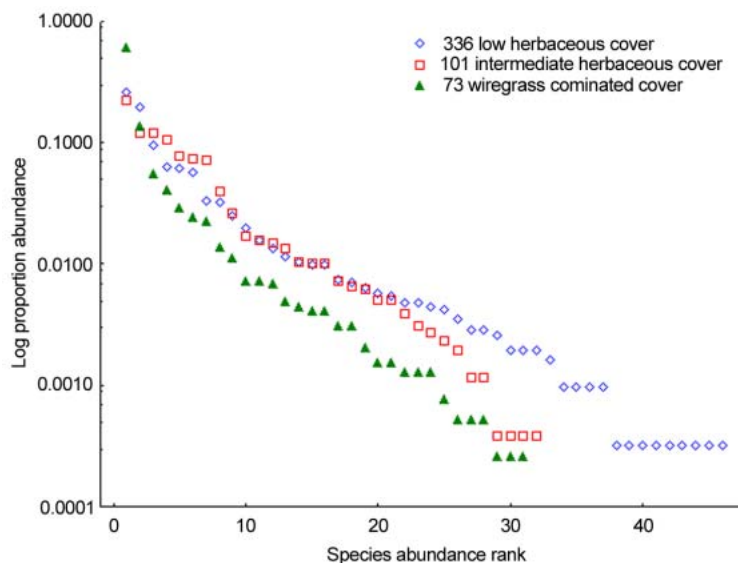


Figure 5. Log abundance-rank plot of pitfall trap data from three sites. Evenness increases in going from high herbaceous (site 73), intermediate herbaceous (101) to low herbaceous (336) ground cover.

Table 1. Ground cover attributes. All numbers are percent cover except the litter scores. The estimate of each plant class coverage was not discounted if there was other vegetation above, below, or intertwined within plants as they were quantified. Therefore summing all the measured classes within a site may give a total coverage > 100%. Litter score is the average litter score of the 56 vegetation samples in a plot. Exposed ground is the average percent of ground not covered by ground cover vegetation. Sites are ordered by their percent herbaceous cover (the sum of *Aristida stricta* and other herbaceous plants).

site	231	336	208	3	7	101	306	322	22	73	79	77
total herbaceous cover	2.4	14.1	28	43.2	49.6	58.3	59.4	63.5	64.4	88	88	89
total woody cover	102.2	73.3	64.2	45.4	67.2	31	62.3	63.4	37	8.1	17	21
<i>Aristida stricta</i>	1.8	10	20.4	41.5	45.2	37.7	43	39.6	53.2	58	67	71
other herbaceous	0.6	4.1	7.5	1.7	4.4	20.6	16.5	24	11.2	31	22	18
<i>Serenoa repens</i>	29.7	12	15.3	10.7	10.2	15.8	19.1	24.2	7.1	1.1	11	18
<i>Ilex</i> sp.	4.2	3.1	15.2	20.6	20.4	12.9	24.6	15.2	26.2	3.3	0.5	1.3
<i>Quercus</i> sp.	57.5	41.8	15.4	5.5	18.3	0.2	4.3	8.1	0	0	4.3	0
other woody	10.8	16.5	18.3	8.6	18.3	2.1	14.2	15.9	3.7	3.7	1.1	1.8
litter score	1.8	1.9	2.5	2.4	2	1.9	1.8	1.8	1.7	2	1.1	2
Exposed ground	18.9	26.8	33.8	19.6	18.4	29.2	19.7	13.7	13.6	12	13	9

(Spearman $r = 0.95$, $p < 0.000$). Other environmental variables, such as the amount of litter (Table 1), the number of longleaf pine trees in a plot (Table 2), and the mean diameter at breast height, show no association with the ground cover/ground-foraging ant community correlation. The amount of exposed ground (Table 1) did tend to decrease with increasing amounts of herbaceous cover but this trend

was not significant.

Ant diversity also changes along with the ground vegetation. Species richness was negatively correlated with percent herbaceous ground cover (Spearman r , using rarefaction species estimates from the pitfall trap data = -0.88 , $p < 0.0001$, Fig. 7). Evenness decreased with decreases in species richness (Fig. 4 and 5) and is therefore

Table 2. Summary of ant sampling data by site and method. Sites are arranged from left to right in order of increasing herbaceous cover.

site	231	336	208	3	7	101	306	322	22	73	79	77
a) Pitfall Traps, 56 traps per site												
# ants captured	3957	3136	2141	2134	2197	2609	1919	1263	1784	3910	1673	2342
# species	43	47	35	38	34	33	36	26	33	32	26	32
b) Ground Baits, 72 baits per site												
% of baits with ants	88%	82%	74%	51%	64%	44%	72%	61%	56%	88%	65%	71%
# ants at baits	3994	1837	2148	899	1145	872	3173	2055	1886	8170	4957	3128
# species	12	17	10	10	12	10	11	8	12	10	4	9
c) Tree Baits												
% occupied baits w/ <i>Crematogaster ashmeadi</i>	85%	91%	96%	98%	99%	91%	85%	89%	99%	32%	90%	96%
# ants at baits	1489	1384	1873	3807	4819	2610	5400	6034	3126	6407	552	1371
# species	7	7	6	6	5	7	8	6	3	10	7	5
# of trees	106	150	144	130	168	282	151	211	121	175	53	107
average DBH	24	24.7	22.7	28.9	22.2	19.1	21.3	18	24.9	20.6	35.6	26.7
d) Subterranean Baits, 72 baits per site												
% of baits with ants	67%	88%	57%	74%	71%	39%	42%	71%	57%	22%	42%	46%
% occupied baits w/ <i>Solenopsis carolinensis</i>	46%	53%	80%	80%	50%	40%	80%	92%	50%	0%	30%	50%
# ants at baits	1212	1110	575	995	638	346	409	1049	556	100	326	355
# species	10	8	6	9	6	6	8	7	6	4	7	4

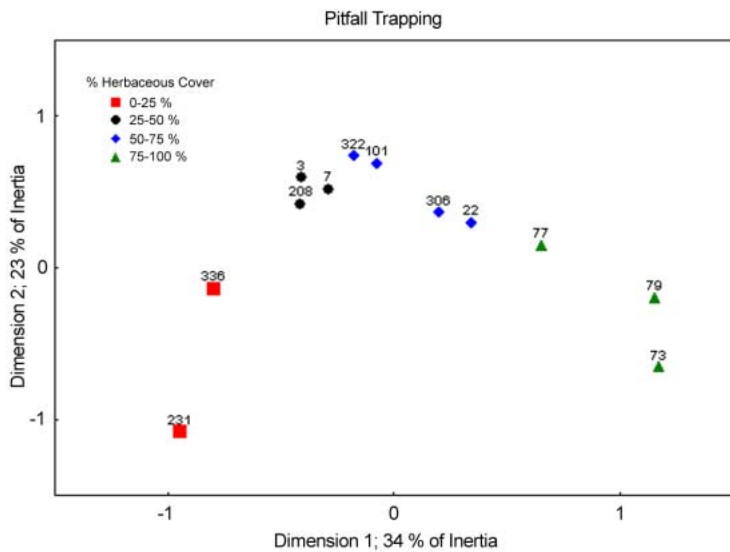


Figure 6. Correspondence analysis ordination of sites for the pitfall trap data. Symbols indicate the percentage of herbaceous cover found at each site. The ant community shows consistent change, in moving from left to right along the first dimension, along the herbaceous ground cover gradient.

also negatively correlated with increasing amounts of herbaceous ground cover.

One way to determine which ant species are important in positioning sites along the ordination axis is to examine how each species' site abundance is correlated with its dimension scores. *Aphaenogaster flemingi*, *C. rimosus*, *Hypoponera opaciceps*, and *S. invicta* are positively correlated with increasing dimension 1 scores and therefore show an increase in abundance with an increasing amount of herbaceous ground cover. *Camponotus floridanus abdominalis*, *Crematogaster cerasi*, *Formica archboldi*, *Leptothorax pergandei*, *Paratrechina parvula*, *Pheidole dentata*, *Pheidole morrisi*, *Pogonomyrmex badius*, *Solenopsis carolinensis*, and *Trachymyrmex septentrionalis* are all negatively correlated with dimension 1 values. These latter species tend to decrease as the amount of herbaceous vegetation increases.

Ground Baiting. Thirty ant species were found among the approximately 34,000 individual ants recorded foraging on 587 baits. The per-site percentage of ant-occupied baits ranged from slightly less than half to close to 90% (Table 2b, Appendix C).

S. invicta, *P. dentata*, and *P. morrisi* were the only species that were both abundant at baits and present at more than a few baits within a site (Table 3). *S. invicta* had a high proportional abundance in 5 sites, obtained the highest proportional abundance scores of any species, and overwhelmingly dominated baits within sites 73 and 79. *P. morrisi* had a high proportional abundance in site 231 and *P. dentata* obtained a moderately high proportional abundance in 4 sites. The latter species also shared a high proportional abundance score with *S. invicta* in site 306 and with *P. morrisi* in site 231.

A number of species with low proportional abundance scores (Table 3) were found at many baits (*Odontomachus brunneus*) or were abundant at the few baits on which they were found (*C. cerasi*, *Crematogaster lineolata*, *Monomorium viride*, *P. moerens*,

P. parvula, and *S. carolinensis*).

Tree Baiting. Close to 1,800 pines were sampled and approximately 39,000 ants from 13 species were found (Table 2c, Appendix D). Eight of these 13 species were rarely sampled on the trees and were more abundant in samples from the ground surface. The true arboreal dwelling species were not commonly encountered using sampling methods other than tree baits. Ants living in the longleaf pines are segregated from those living at and below the ground surface.

The arboreal community is a low diversity assemblage dominated by *C. ashmeadi*. This species was overwhelmingly more abundant than any other arboreal ant (Table 2c, Appendix D), occupying close to half of all the trees baited and making up 80% of the total number of ants sampled on longleaf pines. Other species consistently found on longleaf pine trees include *Camponotus nearticus*, *Leptothorax smithi*, *Solenopsis picta*, and *Forelius pruinosus*.

Correspondence analysis reveals the arboreal community is consistent among most sites. The ordination shows one main cluster of sites (Fig. 8) and two sites (231 and 73) with seemingly divergent arboreal ant communities. *M. viride* was found on five trees scattered within plot 231 and three of these trees yielded only a single *M. viride* forager. Ignoring this aberrant species occurrence, the arboreal ant community in this site is similar to most others. Site 73 had a high abundance of *S. invicta* and *S. picta* and was the only site containing *B. musculus*, *B. obscurior* and *P. moerens*. Three of these five species are exotics. This arboreal ant assemblage was clearly different from that found in other plots.

Subterranean Baiting. Approximately 7,700 individual ants were collected from subterranean baits (Table 2d, Appendix E). Twenty ant species were found among the 485 ant-occupied bait tubes. Ants occupied 56 % of the 864 baits deployed. The remaining tubes either still contained Spam and were presumably

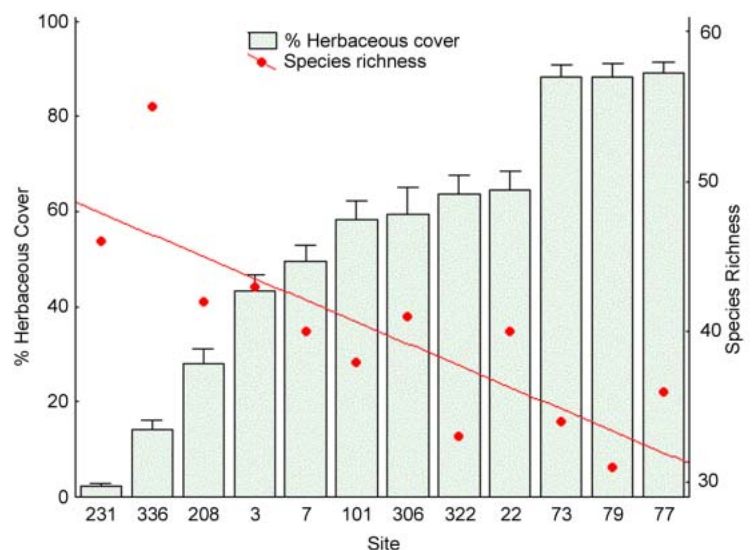


Figure 7. Percent herbaceous cover and rarefaction estimate of species richness by site. Herbaceous cover error bars are \pm 1 SE. The line shown is a best fit line of the species richness data and illustrates the negative correlation of species number and percent herbaceous ground cover.

not found by foraging ants, or the tubes no longer contained any food. As with the arboreal ant species, many of the subterranean species were not commonly encountered using other sampling methods. The subterranean ant community is segregated from other portions of the pine flatwoods ant community. *S. carolinensis* was one exception in being found on a number of ground baits.

The subterranean ant community is primarily composed of *Solenopsis* species from the subgenus *Diplorhoptrum*. *S. carolinensis* was numerically dominant and *S. carolinensis*, *S. abdita*, *S. tonsa*, and *S. tennesseensis* were commonly found in many sites. Two other *Diplorhoptrum*, *S. nickersoni* and *S. pergandi*, were also present but were less commonly encountered. The only other species frequently found foraging on underground baits was *Brachymyrmex depilis*.

Correspondence analysis ordination of these data (Fig. 9) places sites 231, 79, and 73 away from a cluster of similar sites. Samples from site 73 yielded only one *S. carolinensis* and this was the only site containing *P. moerens*. Site 79 also had relatively few *S. carolinensis* but also contained an unusually high number of *S. invicta*. While site 231 contains an abundance of *S. carolinensis*, its ordination position is affected by the highest single site abundance

of *S. nickersoni* and *S. pergandi*.

Discussion

The ground-foraging ant community

In moving from a predominately shrubby ground cover to one dominated by wiregrass, the ground foraging ant community in pine flatwoods becomes less diverse and its species composition changes. Ant community change has been correlated with vegetation change in other studies (Greenslade 1975; Majer 1985; Andersen 1997; Morrison 1998; Bestelmeyer and Wiens 1996) and species turnover tends to increase with increasing habitat divergence. Examining the pine flatwoods' ant community across such a breadth of percent herbaceous cover as we did, the changes we found are not unusual, nor entirely unexpected. Both competitive interactions and environmental conditions within the ant community change across the ground cover gradient and these factors may be important in causing some of the changes we observed.

Competition is known to be important in structuring ant communities (Vepsäläinen and Pisarski 1982; Hölldobler and Wilson 1990). Ants that are abundant, that can monopolize food

Table 3. Abundant ground-foraging ant species. Species shown are those found at many baits or with a high average abundance score within a site. Sites are ordered from low to high herbaceous cover. The top two values in a cell show the total number of baits a species occupied within a site (out of a possible 56) and the average abundance score at those baits. The bottom value in a cell is the proportional abundance score for a species within a site. The derivations of these values are explained in the methods section. The proportional abundances were all multiplied by 100 to eliminate decimal places. Looking at the scores across a row shows how a species' occurrence at baits changes as the amount of herbaceous cover increases. Examining each column reveals the relative dominance of each species within a site.

site	231	336	208	3	7	101	306	322	22	73	79	77
<i>Crematogaster cerasi</i>	4/5 28	1/2 3	3/4 17	1/4.0 6	10/2.6 36							
<i>Crematogaster lineolata</i>					2/3.5 10				1/6.0 8	1/5.0 7	1/2.0 3	
<i>Monomorium viride</i>		2/6.0 17								4/4.3 24		
<i>Odontomachus brunneus</i>	10/1.3 18	17/1.4 32	10/1.2 17	5/1.0 7	1/1.0 1	12/1.5 25	2/1.0 3	4/1.0 6	4/1.3 7			14/1.1 22
<i>Phediole moerens</i>		4/1.3 7		1/1.0 1		1/3.0 4				6/4.0 33		1/5.0 7
<i>Phediole dentata</i>	13/4.3 78	15/2.8 58	23/3.6 114	16/3.2 71	8/3.5 39		18/4.2 104	14/4.6 90	8/3.6 40	3/5.0 21		1/3.0 4
<i>Phediole morrisoni</i>	23/5.3 169	2/5.5 15	9/4.8 60			3/4.3 18						4/3.5 19
<i>Solenopsis carolinensis</i>	2/2.0 6	9/3.0 38	2/3.5 10	3/2.5 10	5/3.0 21	4/4.8 26	2/3.0 8	4/2.0 11	1/4.0 6	1/1.0 1		2/2.0 6
<i>Solenopsis invicta</i>				1/2.0 3	1/5.0 7	2/6.0 17	17/4.4 103	2/3.0 8	15/4.4 92	45/4.2 328	43/4.9 290	18/5.6 139

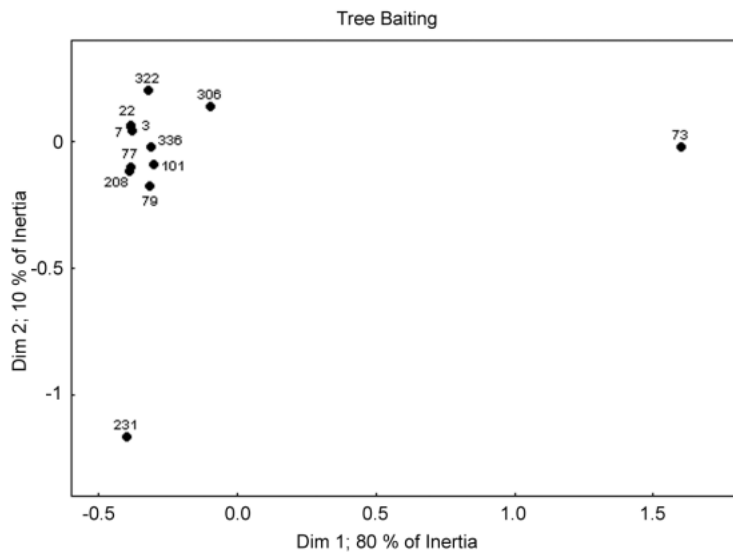


Figure 8. Correspondence analysis ordination of sites for the tree baiting data.

finds, and that prevent other ant colonies from nesting in their vicinity can affect the abundance and distribution of ants found within their resident communities. In high woody and mixed herbaceous-woody ground cover sites, *P. dentata* showed the greatest numerical dominance at ground baits (Table 3, Appendix C). *P. dentata* is known to quickly and aggressively respond to non-nestmate conspecifics and other ant species that it commonly encounters (Carlin and Johnston 1984; Wilson 1975, 1976; Jones and Phillips 1987), illustrating that it is an important behaviorally dominant species. *P. morrisi*, a species closely related to *P. dentata*, also dominated numerous baits in a few high woody cover sites (Table 3, Appendix C) but this ant does not appear to be as strong a

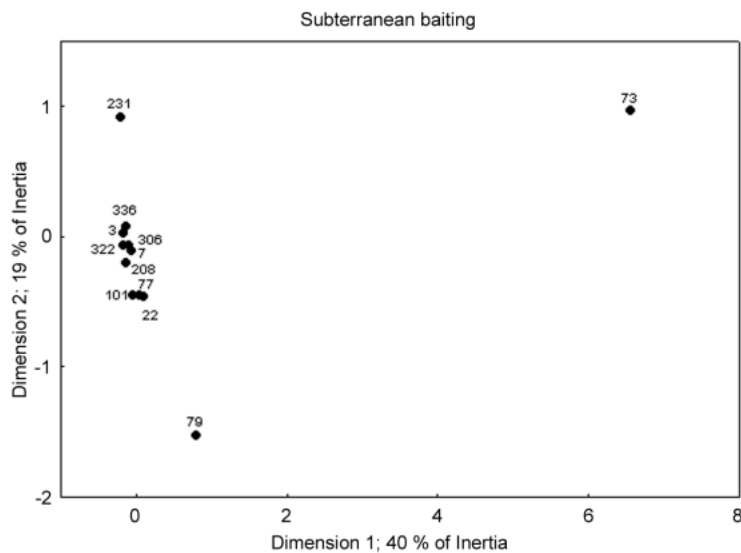


Figure 9. Correspondence analysis ordination of sites for the subterranean baiting data.

competitor as *P. dentata* (Feener 1987). Neither of these *Pheidole* species were found at a majority of the ground baits within any one site and therefore, presuming their appearance at baits is indicative of their nest density and the competitive reach of these two species, their ability to eliminate other co-competitors from the areas they occur in is limited.

In areas with an abundance of wiregrass, *S. invicta* is the dominant ground-foraging ant species (Table 3, Appendix C). This ant defends an absolute territory (Tschinkel et al. 1995), the polygyne form is known to displace other ant species (Porter and Savignano 1990), and it has negative effects on native animals in its introduced range (Tschinkel 1993a; Vinson 1997; Mueller et al. 1999; Allen et al. 2001; Wojcik et al. 2001). This species also has a mature colony size (Tschinkel 1993b) that is an order of magnitude larger (hundreds of thousands versus a maximum of four thousand workers) than *P. dentata* (Calabi and Traniello 1989) and *P. morrisi* (Johnson 1988). In two sites (73 and 79) the fire ant was found at over 75% of the ground bait samples. *S. invicta* is clearly the strongest ant competitor found on the ground surface in the flatwoods and it is likely to have a negative influence on some co-occurring ant species.

Several environmental conditions, including soil moisture, depth to water table and temperature at the ground surface, are likely to vary in parallel with the ground vegetation in pine flatwoods, both as cause and/or as effect. Even seemingly minor changes in these conditions can be important to individual ants and these differences may explain some of the community change we observed (Andersen 1995). Small insects are disproportionately subject to desiccation and therefore are highly sensitive to ambient moisture and temperature differences. Simple ground-shading and plant transpiration changes found across the range of ground cover sampled could create a corresponding gradient of temperature/moisture microclimate conditions at the ground surface. We found that areas dominated by woody plant cover, for example, tend to have more exposed ground. Both sunlight and air movement increases at the ground surface in such areas, creating hotter and dryer conditions on clear, sunny days. Sites dominated by wiregrass, on the other hand, have a thick layer of intertwined grass blades covering most of the ground surface. Such vegetation can protect ants foraging on the ground surface from the more extreme conditions found just above the grass layer. Ant foraging is known to occur within species-typical temperature limits (Whitford and Ettershank 1975; Bernstein 1979; Porter and Tschinkel, 1987) and hence microclimate variation could limit the occurrence of certain species to a portion of the ground cover gradient.

Colony level life history traits are also influenced by, and can depend upon, moisture and temperature conditions. Some ground-nesting ants may be limited to sites with sufficient depth to the water table, making large areas of the flatwoods, with its shallow water table, unusable to them. This may be why such deep-nested species such as *P. badius*, *Prenolepis imparis* and *S. geminata* are essentially absent from the flatwoods. Most ants also require an adequate range of temperature for rearing their brood. It has been shown, for example, that brood development in *S. invicta* occurs only between 22 and 35° C (Porter 1988). Experimental study of environmental variables across the ground cover gradient, and examining how these factors influence particular ant species' distributions, should prove fruitful in explaining some of the

difference we observed in the ground-foraging community.

Arboreal and subterranean ant communities

The arboreal and subterranean ants form two distinctive communities that overlap little with the ground-foraging community or each other, nor are they influenced by changes in ground cover, pine stand characteristics or the ground foraging ant community. Some ground foraging species do venture into these other two zones but their presence is rare and sporadic.

Living in trees or underground requires special adaptations not present in "ordinary," more generalized ground-foraging ants, and probably limit the number of species that live exclusively above and below the ground. Arboreal ants, for example, are on average twice as resistant to desiccation as ground-foraging (even desert) species (Hood and Tschinkel 1990), perhaps because trees do not offer refuge from persistently dry conditions, as soil does. Greater air movement, higher temperature, and increased exposure on trees may exacerbate water loss. Underground, the threat of desiccation is lower but foraging for food can be energetically expensive. The friable, sandy soils we found in most of our plots means constructing and maintaining an anastomosing, ever changing series of tunnels is a constant challenge. The ants foraging on underground baits were small bodied and relatively short-legged, and thus able to move freely within small interstitial soil spaces and soil passages (Kaspari and Weiser 1999) rather than having to build and maintain large passageways. Larger-bodied ants must construct tunnels to forage underground and are unlikely to find enough food to offset the costs incurred by this constant digging. Subterranean army ants of the genus *Nievamymex* do appear to be an exception to this rule. We rarely encountered these ants in our samples but 3 species are resident in the ANF.

The arboreal ant community we found is essentially the same as reported by Tschinkel and Hess (1999). They surveyed a number of pine habitats within the ANF, found little change in community composition among larger longleaf pine trees, and reported *C. ashmeadi* as the dominant species. The arboreal ant assemblage in mature longleaf pine stands appears to be remarkably consistent within and across north Florida pine habitats.

The subterranean foraging ant assemblage is qualitatively similar, in being primarily composed of ants from the tribe *Diplorhoptrum*, to that found in a Gainesville longleaf pine woodland and an adjacent open field (Thompson 1980). *S. carolinensis* was also numerically dominant in both of these sites. Unfortunately Thompson reported limited quantitative data and her study only included a single woodland and open field site. Nevertheless, this limited evidence suggests the flatwoods subterranean ant community may be consistent across a wide geographic area.

Hölldobler and Wilson's (1990) dominance impoverishment rule states that low diversity ant communities are often numerically and behaviorally dominated by a single species. The subterranean and arboreal communities we found conform to this rule. Both consist of a small number of species and each is dominated behaviorally and numerically by a single species, the arboreal community by *C. ashmeadi* (Table 2c) and the subterranean community by *S. carolinensis* (Table 2d). The more diverse ground foraging ant community showed greater variation in the relative abundance of behaviorally and numerically dominant species both

among and between sites, at least for the limited baiting we conducted.

Site 73 had the highest within-site abundance above and below the ground of *Solenopsis invicta*, and was the only site that differed significantly in its arboreal and subterranean ant composition. This flatwoods stand was abiotically aberrant in having a hardened clay layer at least 10 cm thick at the ground surface. The topsoil horizon was hard enough to cause considerable difficulty in digging holes for the subterranean baits. This site was also the only plot within an active cattle-grazing allotment although cows were not observed during our sampling. It is unclear what the interrelationships are among the surface hardpan, cattle grazing, the high abundance of *S. invicta* and the low ant diversity found within this site.

Overall ant diversity

The diversity of the pine flatwoods ant community is remarkable for a Nearctic ant community. The high plot species richness (55 species) and high habitat species richness (72 species) we observed are the highest ever reported for a North American ant community. At a regional scale, this species richness is not as surprising. Florida contains more ant species (218) than many other U.S. states (Mark Deyrup 2003). Faunal surveys from a number of Florida locations have revealed high beta species richness (Van Pelt 1958; Deyrup and Trager 1986; Deyrup et al. 1988; Ferster and Prusak 1994), and new species are still being found (Deyrup 1991; Deyrup and Davis 1998; Deyrup and Lubertazzi 2001).

Florida's high species richness can be partially explained by two factors, biogeography and the presence of many introduced species (Deyrup and Trager 1986, Deyrup 2003). From a biogeographical perspective, elements of ant faunas from the tropical West Indies, temperate North America, and even genera associated with southwestern North American deserts can be found within the state (Deyrup and Trager 1986). Florida also harbors many introduced organisms (Simberloff 1997) including more than 50 exotic ant species (Deyrup, Davis, and Cover 2000). Thorough sampling of other Florida habitats may reveal high ant species richness similar to that of the flatwoods.

The total species richness we found within this habitat may be greater than what was once found in pristine longleaf pine flatwoods. Eight exotic species are present and a number of other species were only found in sites with a ground cover dominated by woody plants. If long term prescribed burning does eventually restore a wiregrass-dominated ground cover to all of our study sites, it is unlikely the within-habitat species richness would remain as high as we observed.

Implications for longleaf pine conservation

Longleaf pine conservation management appears unlikely to produce any change in the arboreal or subterranean ant assemblages. Increasing the age, size, or number of trees may increase the volume of arboreal habitat but these trees will still be inhabited by arboreal ants. Similarly, the subterranean environment does not contain enough differences across our sites that suggest non-subterranean ant specialists are likely to invade this zone.

The most interesting ant community change we observed was associated with the groundcover vegetation; ant diversity at

the ground surface decreased as the percentage of herbaceous ground cover increases. As the continued use of prescribed fire increases the proportion of herbaceous ground cover within the pine flatwoods, presumably ant diversity will decrease in parallel. This will not necessarily be a negative influence of conservation management on ant diversity. It may be that wiregrass dominated vegetation naturally supports fewer ant species than are found in sites with woody plant cover. It is also unlikely that the long-term application of prescribed fires will shift every flatwoods stand to a wiregrass-dominated ground flora. Other factors, such as the depth of the water table, are likely to be just as important in determining the nature of the ground vegetation, and the ants found there, as fire. Provided ANF management plans continue to value sound conservation management practices it is likely this forest will continue to provide longleaf pine stands with a range of ground covers.

More worrisome is the fact that *S. invicta* was found to be abundant in sites that contained an abundance of wiregrass. It seems evident that the herbaceous ground cover in some areas, under the current prescribed fire regime, will be increasingly dominated by wiregrass. It is possible the imported fire ant is displacing native ants from these areas and that its negative effects will increase in these stands. Manipulative experiments excluding this invasive ant are clearly needed to examine these questions.

S. invicta may represent an unquantified negative cost of floral restoration efforts in these forests. With its no-stone-unturned foraging strategy this ant is likely to have direct negative effects on seed dispersal (Zettler et al. 2001; Christian 2001) and many resident invertebrate species (Forys et al. 2001a; Forys et al. 2001b). The diverse collection of native invertebrates (Hanula and Franzreb 1998; Hermann et al. 1998; Landau and Prowell 1999) are also likely to fill specialized ecological roles that help maintain the high floral diversity of longleaf pine habitats. If the fire ant reduces native invertebrate populations this may indirectly harm the flora. Pollination and seed dispersal, for example, are important species interactions that could be affected by abundant fire ant populations.

It would be useful to better understand what factors are allowing the fire ant to thrive in high herbaceous longleaf pine sites. This ant has not previously been associated with natural forest habitats (Tschinkel 1988). *S. invicta* may be responding to favorable resource levels, favorable conditions, or relaxed predation pressure from *Diplorhoptrum* (Buren 1983), or other, ant species in high herbaceous sites. Further study is needed to understand how prevalent this ant is in other sites and to track its abundance through time in areas where prescribed fires are increasing the percentage of herbaceous ground cover.

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Appendix A. Ant species found at each site using all sampling methods.

	Site	3	7	22	73	77	79	101	208	231	306	322	336
Aphaenogaster ashmeadi (Emery)		x	x	x				x	x				x
Aphaenogaster flemingi Smith		x	x	x	x	x	x	x	x		x	x	x
Aphaenogaster floridana Smith										x			
Aphaenogaster treatea Forel			x	x	x		x	x	x	x	x		x
Brachymyrmex depilis Emery		x	x	x	x	x	x	x	x	x	x	x	x
Brachymyrmex musculus Forel					x	x			x				
Brachymyrmex obscurior Forel					x	x				x			x
Camponotus castaneus (Latreille)									x	x	x		x
Camponotus floridanus abdominalis		x	x	x	x	x	x	x	x	x	x	x	x
Camponotus nearcticus Emery					x								x
Camponotus socius Roger				x							x		x
Cardiocondyla wroughtonii (Forel)		x	x	x		x	x	x			x		x
Crematogaster ashmeadi Mayr		x	x	x	x	x	x	x	x	x	x	x	x
Crematogaster cerasi (Fitch)		x	x						x	x	x		x
Crematogaster lineolata (Say)		x	x	x	x		x		x	x	x		x
Crematogaster m. minutissima Mayr		x	x	x					x	x	x	x	x
Crematogaster m. missouriensis Emery		x	x	x		x			x	x	x	x	x
Crematogaster pilosa Emery		x		x	x			x	x		x	x	
Cyphomyrmex rimosus (Spinola)		x	x	x	x	x	x	x	x	x	x	x	x
Dorymyrmex bureni (Trager)					x					x			x
Forelius pruinosus (Roger)		x	x	x	x	x	x	x	x	x	x	x	x
Formica archboldi Smith		x	x	x	x	x		x	x	x	x	x	x
Formica pallidefulva Emery			x	x	x	x	x	x	x	x	x		x
Formica schaufussi dolosa Wheeler		x				x	x	x	x	x	x	x	x
Hypoponera opaciceps (Mayr)		x	x		x	x	x	x		x	x	x	x
Hypoponera opacior (Forel)		x	x	x	x	x	x		x		x		x
Leptothorax a		x	x	x				x	x	x	x	x	x
Leptothorax pergandei Emery		x	x	x	x	x		x	x	x	x	x	x
Leptothorax schauami Roger					x								
Leptothorax texanus Wheeler								x	x	x			x
Leptothorax wheeleri Smith		x	x	x	x	x	x	x	x	x		x	x
Monomorium viride Brown			x	x	x	x	x	x	x	x	x	x	x
Myrmecina americana Emery							x						
Neivamyrmex carolinensis (Emery)						x							x
Neivamyrmex opacithorax (Emery)		x		x				x				x	x
Neivamyrmex texanus Watkins		x						x					
Odontomachus brunneus (Patton)		x	x	x		x		x	x	x	x	x	x
Paratrechina arenivaga (Wheeler)		x	x		x			x	x	x	x		x
Paratrechina concinna Trager											x		
Paratrechina faisonenensis (Forel)		x	x	x	x	x	x	x	x		x	x	x
Paratrechina parvula (Mayr)		x	x	x	x	x		x	x	x	x	x	x
Paratrechina vividula (Nylander)				x				x			x		
Paratrechina wojciki Trager		x	x		x							x	
Pheidole 1				x		x	x		x	x		x	
Pheidole adrianoi Naves										x			
Pheidole dentata Mayr		x	x	x	x	x	x	x	x	x	x	x	x
Pheidole dentigula Smith		x		x		x	x	x	x		x	x	x
Pheidole floridana Emery				x		x			x	x	x		x
Pheidole moerens Wheeler		x		x	x	x		x	x				x
Pheidole metallescens Emery			x					x					x
Pheidole morrissi Forel		x	x		x	x		x	x	x			x
Pheidole vinelandica Forel										x			
Polyergus lucidus Mayr		x	x										
Pogonomyrmex badius (Latreille)										x			x
Pyramica bunki (Brown)			x	x		x	x			x	x		x
Pyramica creightoni (Smith)										x			x
Pyramica dietrichi (Smith)		x	x	x		x	x						x
Pyramica margaritae (Forel)			x	x		x						x	
Pyramica membranifera (Emery)		x	x				x	x		x	x		x
Pyramica talpa (Weber)		x	x			x					x		
Solenopsis abdita Thompson		x	x	x	x	x	x	x	x	x	x	x	x
Solenopsis carolinensis Forel		x	x	x	x	x	x	x	x	x	x	x	x
Solenopsis geminata (Fabricius)									x				
Solenopsis invicta Buren		x	x	x	x	x	x	x	x	x	x	x	x
Solenopsis nickersoni Thompson		x					x			x			x
Solenopsis pergandei Forel				x						x			x
Solenopsis picta Emery		x			x			x	x	x		x	x
Solenopsis tennesseensis Smith		x	x	x		x	x	x	x	x	x	x	x
Solenopsis tonsa Thompson		x	x		x		x			x	x	x	x
Strumigenys louisianae Roger		x		x	x	x	x	x	x	x	x	x	x
Tapinoma sessile (Say)											x	x	x
Trachymyrmex septentrionalis (McCook)										x			x

Appendix B. Pitfall trap species-by-site contingency table.

	3	7	22	73	77	79	101	208	231	306	322	336
Aphaenogaster ashmeadi (Emery)	32	3	1	0	0	0	0	2	0	0	0	17
Aphaenogaster flemingi Smith	20	8	20	17	22	27	1	4	0	24	15	1
Aphaenogaster floridana Smith	0	0	0	0	0	0	0	0	9	0	0	0
Aphaenogaster treatae Forel	0	5	5	5	0	16	5	20	102	4	0	1
Brachymyrmex depilis Emery	31	48	33	44	12	34	44	66	45	24	2	32
Brachymyrmex musculus Forel	0	0	0	54	1	0	0	5	0	0	0	0
Brachymyrmex obscurior Forel	0	0	0	3	1	0	0	0	5	0	0	1
Camponotus castaneus (Latreille)	0	0	0	0	0	0	0	4	2	1	0	9
Camponotus floridanus abdominalis	157	203	113	27	58	18	186	96	97	56	42	194
Camponotus nearcticus Emery	0	0	0	0	0	0	0	0	0	0	0	1
Camponotus socius Roger	0	0	1	0	0	0	0	0	0	10	0	49
Cardiocondyla wroughtonii (Forel)	8	11	14	0	34	12	103	0	0	1	0	42
Crematogaster ashmeadi Mayr	0	2	13	8	4	1	6	9	3	4	8	62
Crematogaster cerasi (Fitch)	42	26	0	0	0	0	0	20	60	2	0	15
Crematogaster lineolata (Say)	61	9	0	88	0	1	0	0	3	0	0	15
Crematogaster m. minutissima Mayr	55	17	1	0	0	0	0	12	2	51	21	18
Crematogaster m. missouriensis Emery	7	24	4	0	1	0	0	13	2	3	3	9
Crematogaster pilosa Emery	17	0	0	16	0	0	17	3	0	5	15	0
Cyphomyrmex rimosus (Spinola)	8	4	28	95	44	210	27	5	9	14	8	11
Dorymyrmex bureni (Trager)	0	0	0	12	0	0	0	0	25	0	0	3
Forelius pruinus (Roger)	107	407	54	112	301	115	35	140	33	153	337	78
Formica archboldi Smith	7	18	14	2	8	0	26	11	15	10	1	31
Formica pallidefulva Emery	0	43	1	6	3	1	1	13	5	2	0	14
Formica schaufussi dolosa Wheeler	123	0	0	0	1	0	200	62	12	2	2	22
Hypoponera opaciceps (Mayr)	1	4	0	12	15	26	3	0	4	9	3	0
Hypoponera opacior (Forel)	1	9	2	2	8	4	0	2	0	5	0	6
Leptothorax a	1	0	1	0	0	0	7	18	7	2	3	1
Leptothorax pergandei Emery	4	26	0	16	2	0	26	38	112	4	10	103
Leptothorax schaumii Roger	0	0	0	1	0	0	0	0	0	0	0	0
Leptothorax texanus Wheeler	0	0	0	0	0	0	3	1	5	0	0	31
Monomorium viride Brown	0	0	2	528	0	0	0	0	412	0	1	13
Myrmecina americana Emery	0	0	0	0	0	4	0	0	0	0	0	0
Neivamyrmex carolinensis (Emery)	0	0	0	0	1	0	0	0	0	0	0	5
Neivamyrmex opacithorax (Emery)	10	0	1	0	0	0	41	0	0	0	13	23
Neivamyrmex texanus Watkins	1	0	0	0	0	0	39	0	0	0	0	0
Odontomachus brunneus (Patton)	113	81	96	0	45	0	192	44	51	116	73	179
Paratrechina arenivaga (Wheeler)	1	10	0	6	0	0	10	2	617	0	0	6
Paratrechina concinna Trager	0	0	0	0	0	0	0	0	0	6	0	0
Paratrechina faisonensis (Forel)	43	97	211	28	142	82	68	145	0	89	60	36
Paratrechina parvula (Mayr)	0	0	0	1	0	0	16	0	380	0	0	301
Paratrechina vividula (Nylander)	0	0	2	0	0	0	19	0	0	8	0	0
Paratrechina wojciki Trager	18	4	0	28	0	0	0	0	0	0	0	0
Pheidole 1	0	0	3	0	4	1	0	0	7	0	0	0
Pheidole adrianoi Naves	0	0	0	0	0	0	0	0	4	0	0	0
Pheidole dentata Mayr	867	124	113	19	182	5	309	499	543	491	182	198
Pheidole dentigula Smith	6	0	1	0	1	5	1	3	0	4	2	6
Pheidole floridana Emery	0	0	74	0	0	6	0	6	6	4	0	20
Pheidole metallescens Emery	0	5	0	0	0	0	274	0	0	0	0	0
Pheidole moerens Wheeler	0	0	14	157	1	0	13	5	0	0	0	0
Pheidole morrisoni Forel	63	127	0	1	1	0	0	195	585	0	0	101
Pogonomyrmex badius (Latreille)	0	0	0	0	0	0	0	0	5	0	0	3
Polyergus lucidus Mayr	3	1	0	0	0	0	0	0	0	0	0	0
Pyramica bunki (Brown)	0	1	5	0	1	2	0	0	3	7	0	8
Pyramica creightoni (Smith)	0	0	0	0	0	0	0	0	3	0	0	1
Pyramica dietrichi (Smith)	12	1	1	0	1	1	0	0	0	0	0	3
Pyramica margaritae (Forel)	0	1	1	0	7	0	0	0	0	0	3	0
Pyramica membranifera (Emery)	2	1	0	0	0	4	8	0	1	1	0	1
Pyramica talpa (Weber)	6	1	0	0	2	0	0	0	0	1	0	0
Solenopsis abdita Thompson	4	0	0	0	0	0	0	0	14	0	0	0
Solenopsis carolinensis Forel	290	844	459	217	416	102	586	673	356	295	415	821
Solenopsis geminata (Fabricius)	0	0	0	0	0	0	0	1	0	0	0	0
Solenopsis invicta Buren	3	15	481	2355	1014	976	312	8	4	489	2	0
Solenopsis nickersoni Thompson	0	0	0	0	0	2	0	0	344	0	0	620
Solenopsis pergandei Forel	0	0	0	0	0	0	0	0	1	0	0	0
Solenopsis picta Emery	0	0	0	2	0	0	1	0	0	0	0	0
Solenopsis tennesseensis Smith	6	0	0	0	0	0	0	0	0	0	0	0
Solenopsis tonsa Thompson	1	0	0	5	0	0	0	1	3	0	0	1
Strumigenys louisianae Roger	1	0	3	5	8	1	13	7	1	3	1	1
Tapinoma sessile (Say)	0	0	0	0	0	0	0	0	0	14	38	0
Trachymyrmex septentrionalis (McCook)	0	0	0	0	0	0	0	0	3	0	0	3

Appendix C. Ground bait species-by-site contingency table.

	3	7	22	73	77	79	101	208	231	306	322	336
Aphaenogaster ashmeadi (Emery)	30	0	0	0	0	0	14	0	0	0	0	10
Aphaenogaster flemingi Smith	0	0	2	57	7	0	0	0	0	4	172	0
Aphaenogaster treatae Forel	0	0	0	0	0	23	0	5	1	0	0	18
Camponotus floridanus abdominalis	14	15	10	0	20	0	17	4	10	11	0	1
Crematogaster cerasi (Fitch)	49	99	0	0	0	0	0	95	311	0	0	3
Crematogaster lineolata (Say)	0	37	150	55	0	2	0	0	0	0	0	0
Crematogaster pilosa Emery	5	0	16	86	0	0	0	0	0	0	0	0
Dorymyrmex bureni (Trager)	0	0	0	0	0	0	0	0	0	0	0	1
Formica archboldi Smith	0	2	0	0	0	0	0	0	0	0	0	0
Forelius pruinus (Roger)	0	443	2	7	0	7	0	0	0	225	0	0
Leptothorax a	0	1	0	0	0	0	0	0	0	0	0	0
Leptothorax pergandei Emery	0	5	1	0	0	0	0	2	0	1	0	4
Leptothorax texanus Wheeler	0	0	0	0	0	0	0	0	0	0	0	1
Monomorium viride Brown	0	0	0	226	0	0	0	0	0	0	0	730
Odontomachus brunneus (Patton)	5	1	5	0	16	0	19	12	13	2	4	23
Paratrechina arenivaga (Wheeler)	0	0	0	0	0	0	34	5	3	16	0	0
Paratrechina faissonensis (Forel)	43	2	18	8	51	0	0	33	0	10	155	3
Paratrechina parvula (Mayr)	0	0	0	0	0	0	73	0	50	0	0	112
Paratrechina vividula (Nylander)	0	0	14	0	0	0	0	0	0	6	0	0
Paratrechina wojciki Trager	0	0	0	0	0	0	0	0	0	0	1	0
Pheidole dentata Mayr	737	299	460	200	14	0	0	1172	981	1040	1469	407
Pheidole adrianoi Naves	0	0	0	0	0	0	0	0	47	0	0	0
Pheidole vinelandica Forel	0	0	0	0	0	0	0	0	23	0	0	0
Pheidole metallescens Emery	0	0	0	0	0	0	9	0	0	0	0	11
Pheidole moerens Wheeler	1	0	0	259	73	0	8	0	0	0	0	5
Pheidole morrisi Forel	0	0	0	0	212	0	135	669	2479	0	0	219
Solenopsis carolinensis Forel	12	183	30	1	15	0	281	151	16	31	23	288
Solenopsis invicta Buren	3	58	1178	7271	2720	4925	282	0	0	1827	12	0
Solenopsis nickersoni Thompson	0	0	0	0	0	0	0	0	60	0	0	0
Tapinoma sessile (Say)	0	0	0	0	0	0	0	0	0	0	219	1

Appendix D. Tree bait species-by-site contingency table.

	3	7	22	73	77	79	101	208	231	306	322	336
Brachymyrmex musculus Forel	0	0	0	291	0	0	0	0	0	0	0	0
Brachymyrmex obscurior Forel	0	0	0	5	0	0	0	0	0	0	0	0
Camponotus castaneus (Latreille)	0	0	0	0	0	0	0	0	0	1	0	0
Camponotus floridanus abdominalis	0	0	0	1	0	0	0	0	2	10	0	0
Camponotus nearcticus Emery	8	1	0	22	32	2	87	3	30	2	13	7
Crematogaster ashmeadi Mayr	3732	4789	3093	2044	1312	514	2382	1793	1269	4589	5385	1253
Forelius pruinus (Roger)	28	13	20	54	3	1	42	5	1	235	499	49
Leptothorax schaumii Roger	4	0	0	0	0	1	4	0	0	1	0	4
Leptothorax smithi Smith	28	13	13	4	22	14	18	65	69	0	11	34
Monomorium viride Brown	0	3	0	0	2	5	8	3	108	12	8	2
Pheidole moerens Wheeler	0	0	0	75	0	0	0	0	0	0	0	0
Solenopsis invicta Buren	0	0	0	2114	0	15	0	0	0	550	0	0
Solenopsis picta Emery	7	0	0	1797	0	0	69	4	10	0	118	35

Appendix E. Subterranean bait species-by-site contingency table.

	3	7	22	73	77	79	101	208	231	306	322	336
Brachymyrmex depilis Emery	46	84	23	0	0	10	4	13	13	7	10	35
Crematogaster lineolata (Say)	9	0	0	0	0	0	0	0	0	0	0	0
Crematogaster m. missouriensis Emery	4	0	0	0	0	0	0	0	0	0	0	0
Forelius pruinus (Roger)	0	0	0	0	0	0	0	0	0	0	3	0
Hypoponera opaciceps (Mayr)	0	5	0	0	0	0	0	0	0	15	0	8
Monomorium viride Brown	0	0	0	0	0	0	0	0	30	0	0	0
Paratrechina faissonensis (Forel)	0	0	0	0	0	2	0	2	0	0	1	0
Pheidole 1	0	0	0	0	0	0	0	1	15	2	0	0
Pheidole dentata Mayr	0	0	0	0	0	0	0	0	12	20	0	0
Pheidole dentigula Smith	1	0	0	0	0	0	0	0	0	0	0	1
Pheidole metallescens Emery	0	0	0	0	0	0	10	0	0	0	0	0
Pheidole moerens Wheeler	0	0	0	55	0	0	0	0	0	0	0	0
Pheidole morrisi Forel	0	0	0	0	0	0	0	0	42	0	0	0
Solenopsis abdita Thompson	1	185	6	14	71	3	58	7	51	11	15	83
Solenopsis carolinensis Forel	789	341	291	1	165	83	151	451	560	314	960	584
Solenopsis invicta Buren	0	0	61	30	14	138	1	0	0	13	0	0
Solenopsis nickersoni Thompson	40	0	0	0	0	0	0	0	159	0	0	0
Solenopsis pergandei Forel	0	0	41	0	0	0	0	0	268	0	0	148
Solenopsis tennesseensis Smith	35	2	134	0	105	73	122	101	62	0	40	121
Solenopsis tonsa Thompson	70	21	0	0	0	17	0	0	0	27	20	130