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Habitat disturbance and the diversity and abundance of ants (Formicidae) in the Southeastern Fall-Line Sandhills

John H. Graham¹, Hoyt H. Hughie¹, Susan Jones^{1,2}, Kerri Wrinn^{1,3}, Anthony J. Krzysik⁴, Jeffrey J. Duda⁵, D. Carl Freeman⁶, John M. Emlen⁵, John C. Zak⁷, David A. Kovacic⁸, Catherine Chamberlin-Graham¹, and Harold Balbach⁹

¹Department of Biology, Berry College, Mount Berry, Georgia 30149

²Tall Timbers Research Station, Tallahassee, Florida 32312-0918

³University of Cincinnati, Cincinnati, Ohio 40121

⁴Prescott College, Prescott, Arizona 86301

⁵USGS Biological Resources Division, Western Fisheries Research Center, Seattle, Washington 98115

⁶Department of Biological Sciences, Wayne State University, Detroit, Michigan 48202

⁷Department of Biology, Texas Tech University, Lubbock, Texas 79409

⁸Department of Landscape Architecture and Natural Resources and Environmental Sciences, University of Illinois, Champaign, Illinois 61820

⁹U. S. Army ERDC-CERL, Champaign, Illinois 61826

jgraham@berry.edu

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Abstract

We examined habitat disturbance, species richness, equitability, and abundance of ants in the Fall-Line Sandhills, at Fort Benning, Georgia. We collected ants with pitfall traps, sweep nets, and by searching tree trunks. Disturbed areas were used for military training; tracked and wheeled vehicles damaged vegetation and soils. Highly disturbed sites had fewer trees, diminished ground cover, warmer soils in the summer, and more compacted soils with a shallower A-horizon. We collected 48 species of ants, in 23 genera (141,468 individuals), over four years of sampling. Highly disturbed areas had fewer species, and greater numbers of ants than did moderately or lightly disturbed areas. The ant communities in disturbed areas were also less equitable, and were dominated by *Dorymyrmex smithi*.

Keywords: ecological communities, landscape disturbance, military training, species richness, upland mixed pine-hardwoods forest

Introduction

Ants have numerous advantages over vertebrates and other arthropods in studies of landscape disturbance and species diversity. They occur throughout the world, are easily collected, are taxonomically well known, and constitute an important fraction of the animal biomass in terrestrial ecosystems (Fittkau and Klinge 1973; Lynch et al. 1988; Hölldobler and Wilson 1990). They also respond to stress on a much finer scale than do vertebrates (Andersen 1997b). Moreover, ants perform major ecological functions (Wheeler 1910; Hölldobler and Wilson 1990). They are typically the dominant predators and scavengers in their size range (Jeanne 1979; Fellers 1987). Ants are often more important than earthworms for soil mixing, nutrient transport, and soil aeration (Lyford 1963; Gentry and Stiritz 1972). Moreover, they are major granivores in arid regions (MacMahon et al. 2000), and are important for pollination (Hickman 1974), dispersal (Beattie and Culver 1981), and protection (Janzen 1966) of numerous plants. Ants, for example, are responsible for the dispersal of a third of herbaceous plants in New York forests (Handel et al. 1981). Here we examine ant

communities along a disturbance gradient at Fort Benning, an Army installation in the Fall-Line Sandhills of west-central Georgia, to assess their response to landscape disturbance.

Previous research suggests that ant communities in other localities respond predictably to disturbance (Majer 1983; Andersen 1990, 1997a, b; Bestelmeyer and Wiens 1996; Majer and Nichols 1998; Peck et al. 1998; Bisevac and Majer 1999; Agosti et al. 2000; Mitchell et al. 2002). Their diversity and composition, for example, have been used for more than 20 years in Australia to monitor the restoration of landscapes damaged by mining. Andersen (1997a), King et al. (1998), and Majer and Nichols (1998) found that ant communities in damaged ecosystems have lower species diversity and greater numbers of Dolichoderines (a subfamily of particularly active ants). Do ant communities in the southeastern United States show a similar response to disturbance?

Ants are a well-defined component of the invertebrate community, one of nine proposed ecological indicators we are evaluating at Fort Benning to develop classes of metrics that define a disturbance gradient. The other indicators are habitat structure and condition, soil physical properties, soil chemistry, nutrient leakage

and dynamics, soil microbial community, developmental instability (Duda et al. 2003, Freeman et al., 2004 and in press, a, b), plant physiology (Duda et al. 2003; Freeman et al., in press, b), and woody ground cover spatial dynamics.

Materials and Methods

Study Area

The Fall-Line Sandhills are a narrow band of rolling hills between the Piedmont and Coastal Plain; they extend from west-central Georgia and adjacent Alabama to southeastern North Carolina. The soils are sandy—low in nutrients and easily eroded. The pre-settlement forest consisted of mixed pines (shortleaf, loblolly, and longleaf) and hardwoods (especially oak and hickory), and was transitional to the longleaf pine-wiregrass or bluestem pyroclimax community on the lower Coastal Plain, where fire was more frequent (Frost 1993; Skeen et al. 1993). All of our research sites and the surrounding landscape, however, were subjected to agricultural activities prior to the 1940s (Kane and Keeton 1998). Loblolly pine is now the dominant pine, partly because post-agricultural silviculturists favored it. Currently, Fort Benning has an active three-year burn cycle, specifically addressing requirements of the recovery plan for the federally endangered Red-cockaded Woodpecker (*Picoides borealis*) and associated longleaf pine (*Pinus palustris*). The ground cover is more diverse here than in the lower Coastal Plain, consisting primarily of woody vegetation (tree seedlings, shrubs, and vines) along with perennial forbs and some grasses (though not wiregrass, *Aristida stricta*).

Today, stands of mature longleaf pine in the southeastern United States have been reduced to less than three percent of their former range (Ware et al. 1993). Many of the remnant stands are in the Fall-Line Sandhills, serving as a refuge for species of concern, including the Red-cockaded Woodpecker and gopher tortoise (*Gopherus polyphemus*). Although none of the ants of the Fall-Line Sandhills are endangered (most ants are generalists), they nevertheless respond to the same disturbances that influence the better-known vertebrates and dominant plants. Moreover, arboreal ants, such as *Crematogaster ashmeadi*, are an important food of the Red-cockaded Woodpecker (McFarlane 1992; Hess and James 1998).

Fort Benning is one of several military bases on the Fall-Line Sandhills. Military lands collectively support many of the largest and least disturbed stands of longleaf pine and turkey oak (*Quercus laevis*) in the southeastern United States. Certain parts of Fort Benning, however, are heavily disturbed by mechanized infantry training. Tanks and other tracked vehicles have denuded some large areas of most, or all, of their vegetation. Because one can find relatively undisturbed forest adjacent to such training areas, it is possible to study ant communities across a steep disturbance gradient.

Disturbance Regimes

The disturbance gradient was initially divided into three classes: high, medium, and low (Figure 1). Heavily disturbed areas had greatly reduced plant cover, large patches of bare ground, thinner soil A-horizons, gullies, rock pedestals, and other signs of active erosion. There was also abundant evidence of recent mechanized

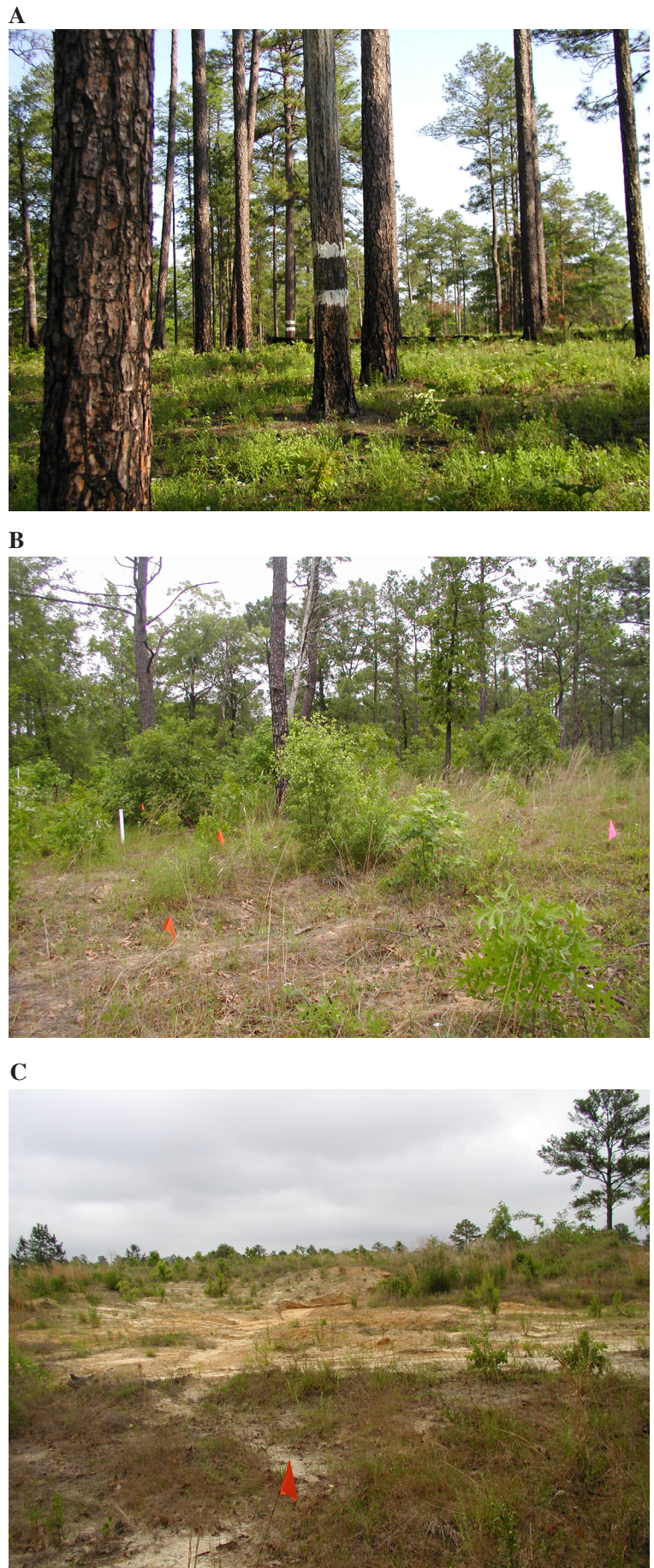


Figure 1. Sample sites at Fort Benning, Georgia. (A) Low disturbance site, L1. (B) Medium disturbance site, M2. (C) High disturbance site, H1.

infantry training (tank tracks, concertina wire, empty shell casings, etc.). Moderately disturbed areas had an intact canopy, well-established ground cover, and fewer signs of active erosion. Nevertheless, gullies were present and there was evidence of surface soil loss. There was also much less evidence of vehicle use. Lightly disturbed areas had minimal disturbance to soils, extensive ground cover (especially with woody vegetation), and the highest tree densities and canopy cover. There were also no signs of recent erosion. Moreover, there was little or no evidence of off-road vehicle and infantry use, except on well-established trails.

Research Sites

We established nine upland mixed pine-hardwoods forest sites in two adjacent third-order watersheds—three in each disturbance class (Table 1). All sites were in Troup-Cowarts-Nankin Loamy-Sand soils (NRCS 1997). Six sites (two sets of the three disturbance classes) were in the Bonham Creek watershed and three were in the Sally Branch watershed. Elevations ranged from about 100 m to more than 150 m above sea level. High disturbance sites (H1, H2, H3) are currently used for landscape-scale training of mechanized infantry. Medium disturbance sites (M1, M2, M3) may have experienced similar activities in the recent past, but current use consists of foot traffic. Vehicles are confined to existing roads and trails. Low disturbance sites (L1, L2, L3) are not being used for military training. They are protected either for conservation and compliance, or because they are in the safety fans of artillery ranges. L3, M3, and H3 were in the Sally Creek Drainage; all other sites were in the Bonham Creek Drainage.

Physical Habitat

At each site (in 2001 and 2002), we sampled soil A-horizon depth (mm), soil compaction (Lang Penetrometer Units), soil shear stress (kg/cm²), bare ground (%), forb cover (%), grass cover (%), woody ground cover (%), mean diameter breast height of trees (dbh in cm), canopy cover (%), basal area of trees (m²/ha), sapling density (number per 3600 m²), and tree density, small tree density, medium tree density, and large tree density (all in number per 3600 m²). We also measured percent soil moisture (Bonham Creek sites in May and November 2000 and 2001, and at all sites in

May and November 2002). In 2002 and 2003, we sampled air and soil temperatures with continuous recorders, located at L1, L2, M1, M2, H1, and H2. The air temperatures were taken 1 m above the soil surface. Soil temperatures were taken 15 cm below the soil surface.

Fire Frequency

We determined the fire frequency for each site, over a 23-year period (1980-2002). Fort Benning Forestry and Natural Resources Offices provided data on fire coverage by forest tract and year (1980-1999). We placed these data into Geographic Information Systems (GIS) data layers. Data for some years were missing. For prescribed burns, we had data from 1980-1988, 1991-1994, and 1997-1999. For wildfires, we had data for 1980-1994 and 1997-1999. We were present in the years 2000-2002 to verify recent fires.

Sampling of Ants

We collected ants by pitfall trap over four years (2000-2003) and sweep net over three years (2000-2002). We also hand sampled ants on tree trunks in 2002. All samples were collected in late April through May of each year, to minimize seasonal variation and because of limited site accessibility due to military use at other times.

Pitfall traps (9 ounce Solo® plastic cups, 7 cm diameter) were set out in clusters of five. Within each cluster, traps were separated by about 3 m. Propylene glycol (Sierra Antifreeze) was used to trap and preserve the ants. Traps were deployed overnight, for 24 hours duration. (The short trap time was necessitated by the difficulty of arranging access to a particular site on more than two consecutive days.) At no time during the sampling, in any of the four years, was there rain during a 24-hour sampling period. Following collection, the ants were transferred to 80 percent ethanol for final preservation.

In 2000, 2002, and 2003, we sampled three sites within each disturbance regime. Numbers of samples (clusters) per site varied from year-to-year: four clusters per site in 2000 and 2003, five clusters per site in 2001, and six clusters per site in 2002. In 2001 we sampled only two sites within each disturbance regime.

Table 1. Sampling sites at Fort Benning, Georgia.

Site	Disturbance	Drainage	Latitude	Longitude
L1	Low	Bonham Creek	32° 24.719 N	84° 45.642 W
L2	Low	Bonham Creek	32° 23.529 N	84° 45.766 W
M1	Medium	Bonham Creek	32° 24.034 N	84° 45.821 W
M2	Medium	Bonham Creek	32° 25.095 N	84° 44.712 W
H1	High	Bonham Creek	32° 24.433 N	84° 44.329 W
H2	High	Bonham Creek	32° 24.385 N	84° 45.208 W
L3	Low	Sally Branch	32° 26.052 N	84° 44.410 W
M3	Medium	Sally Branch	32° 24.847 N	84° 44.163 W
H3	High	Sally Branch	32° 24.699 N	84° 44.235 W

Sweep netting was also used to collect ants on herbs and shrubs. Working in the same 4-hectare area as the pitfall traps, we used heavy-duty muslin nets, counting one complete sweep as a figure-eight movement of the net through vegetation. As with the pitfall traps, the intensity of sampling varied from year to year. In 2000, we collected two samples of 100 sweeps at each site. In 2001 and 2002, we collected four samples of 50 sweeps at each site. We did not sample with sweep nets in 2003.

We conducted a survey of *Crematogaster ashmeadi*, and other arboreal ants, on pines and oaks at our research sites in May 2002. A team of three searched the lower trunks of pines and oaks and collected ants with an aspirator. Searching involved picking and probing of the bark. If no ants were encountered on a particular tree, neighboring trees of the same type were searched until 10 minutes had elapsed. Time walking from tree-to-tree was disregarded. We defined a sample as all the ants collected during 10 minutes of searching. At each site, we obtained four samples from oaks and four samples from pines.

Ants were identified to genus using Hölldobler and Wilson (1990) and Bolton (1997), and then to species using Creighton's (1950) *The Ants of North America* and more specific taxonomic works, including Trager's (1984) review of *Paratrechina*, Buren's (1958, 1968) review of *Crematogaster*, DuBois's (1986) review of *Monomorium*, Trager's (1988) and Snelling's (1995) reviews of *Dorymyrmex* (*Conomyrma*), Wilson's (2003) review of *Pheidole*, and online keys to *Aphaenogaster*, *Camponotus*, *Crematogaster*, *Hypoponera*, and *Temnothorax* (*Leptothorax*) by William and Emma Mackay (2004). All species names are those given in Bolton's (1995) *A New General Catalogue of the Ants of the World*, except where more recent taxonomic works were available. Voucher specimens will be deposited with the Georgia Museum of Natural History, Athens, Georgia. A photographic guide to the ants of Fort Benning is available online at <http://fsweb.berry.edu/academic/mans/jgraham/>. Species identifications have been verified by Stefan Cover (Museum of Comparative Zoology, Harvard University) and Mark Deyrup (Archbold Biological Station), from these photographs.

Statistical Analysis

For each sample (cluster) we counted the total number of species (*S*) and individuals (*N*). From the relative abundances of each species, we also computed the Shannon-Wiener Index of Equitability E_H (Whittaker 1975), which is a measure of the uniformity of species frequencies. E_H equals H'/H'_{max} , where $H' = -\sum p_i \log p_i$ and $H'_{max} = \log S$. The frequency of species *i* in a sample is p_i .

Because ant communities in the same nine sites were sampled in three of the four years (2000, 2002, and 2003 for pitfalls, and 2000, 2001, 2002 for sweeps), the experimental design was a within-subjects (repeated-measures) design (Crowder and Hand 1990; von Ende 1993). Sites (a random effect) were nested within disturbance classes, and samples (clusters) were nested within sites. We used a repeated-measures analysis of variance (General Linear Model, SPSS Inc.) to test the hypotheses that *S*, *N*, and E_H did not differ among disturbance classes. *N* was log transformed, and E_H was arcsine transformed, prior to the analysis. Univariate ANOVA is generally insensitive to heteroscedasticity and to skewed distributions (Lindman 1992), as is Tamhane's T2 test (Tamhane 1979) if the null hypothesis is rejected. For multiple comparisons, we used Student-Newman-Keuls *post hoc* test when variances were homogeneous, and Tamhane's T2 when they were not. To correct for multiple tests, we used the sequential Bonferroni procedure to calculate a table-wide significance level (Rice 1989).

Results

We identified and counted 137,355 ants in pitfall traps, 1,295 in sweep nets, and 2,818 on trunks of pine and oak. These represented 48 species in 23 genera (Appendices A, B, C, D).

Physical Habitat

As previously noted, vegetation and soils in the three disturbance regimes differed (Table 2). The most significant differences were in soil A-horizon depth and soil compaction. Less disturbed sites had deeper and less compacted soils. Highly disturbed

Table 2. Physical habitat characteristics of the study sites. Values are means.

Variable	Sites									Sample Size (<i>N</i>)
	L1	L2	L3	M1	M2	M3	H1	H2	H3	
A-Horizon Soil Depth (mm)	15.5	16.5	15	6.99	9.34	15.4	0.765	1.91	5.22	34
Soil Compaction (Lang Units)	3.86	4.36	4.97	6.59	3.95	5.72	8.81	6.93	7.64	240
Soil Shear Strength (kg/cm ²)	3.64	2.98	2.77	4.28	2.2	2.35	3.07	2.3	2.97	40
Bare Soil (%)	17	24.7	15.2	45.7	40	22	52.6	74.8	44.4	6
Forbs (%)	6.35	10.1	4.1	10.1	6.54	7.02	5.22	8.41	6.58	6
Grass (%)	5.7	6.48	0.34	3.31	4.27	4.26	8.46	3.6	2.18	6
Woody Plants (%)	28.4	30	12.1	18.2	11.1	17.5	14.3	6.19	8.49	6
Diameter Breast Height (cm)	15.2	17.9	19.1	17.6	18.5	40.4	12.3	11	30.6	47-221
Number of Trees per 3600 m ²	55.3	35	31.8	38.3	17	11.8	14.8	16.3	13.5	4
Canopy Cover (%)	47.1	48.3	54.6	56.6	29.3	48.1	4.04	19.9	30.9	10
Basal Area (m ² /ha)	22	12.9	25.7	22	3.67	18.4	0	0	11	5
Sapling Density (number/3600 m ²)	6.2	6.8	6.8	6.2	5.4	8.6	1	1.6	5.8	5
Small Tree Density (number/3600 m ²)	6.2	3.4	6	5.6	3.4	4.8	0.4	0.8	3.4	5
Medium Tree Density (number/3600 m ²)	2	0.8	1.2	2.2	1.4	1.2	0	0	1.4	5
Large Tree Density (number/3600 m ²)	2.4	1.4	2.8	2.4	0.4	2	0	0	1.2	5

sites differed from the lightly and moderately disturbed sites in that they had fewer large trees (as measured by canopy cover, basal area, dbh, and density of trees), more bare ground, and a less diverse ground cover. Lightly disturbed sites had a higher tree density than moderately or heavily disturbed sites. Percent soil moisture (arcsine transformation) showed significant variation among sites ($F = 10.82$, $df = 8, 462$, $P < 0.001$). It was less than 11% at all sites (range: < 0.5 to 24%). M1 was significantly wetter than L1, L2, M2, and H2 (Tamhane's T2, $P < 0.05$). The wettest year was 2002. Seasonal soil moisture varied unpredictably with year and month.

There was a significant interaction between month and disturbance regime on average maximum soil temperature ($F = 7.762$, $df = 4, 24$, $P < 0.001$). In January, there was very little difference in soil temperature among the three disturbance regimes (H1 and H2 had maximum temperatures that were 0.23° C cooler than L1 and L2). By May, however, H1 and H2 had daily maximum soil temperatures that were 4.9 to 5.8° C warmer than those at M1, M2, L1, and L2. In July, daily maximum temperatures at H1 and H2 were 5.2 to 5.3° C warmer than those at M1, M2, and L1. The air temperatures in May, however, which were taken 1 m above the soil surface, were only 0.60° C warmer at H1 and H2.

The highly disturbed sites had a very different temperature profile during the summer. They stored heat, so that the maximum soil temperature exceeded the maximum air temperature sometime in April or May and remained that way until September or October. In the lightly and moderately disturbed sites, the maximum soil temperature never exceeded the maximum air temperature.

Fire Frequency

The average time between wildfires at a given site was 15.07 ± 8.19 years (mean ± standard deviation), and the average time between prescribed burns was 3.84 ± 1.71 years. Ignoring the source of the fire, the average time between burns was 3.24 ± 1.66 years. There was no significant association between fire (none, wildfire, prescribed) and disturbance class ($\chi^2 = 7.162$, $df = 4$, $P = 0.128$).

Ant Diversity and Abundance

Ground-Dwelling Ants

We collected 137,355 ants (44 species) in our pitfall samples (Appendix A). There were significant differences in species richness (S), equitability (arcsine E_H), and abundance (log N) among the three disturbance classes (Tables 3-5, Figure 2). The highly disturbed sites had fewer species of ants (Tamhane T2, $P < 0.05$) and lower equitability (Tamhane T2, $P < 0.05$). Species richness was greater in the moderately disturbed sites than in the lightly disturbed sites, but the difference was not statistically significant (Tamhane T2, $P > 0.05$). The highly disturbed sites also had more ants than the moderately disturbed sites, which in turn had more ants than the lightly disturbed sites (Tamhane T2, $P < 0.05$). There were significant differences in species richness among sites, and significant differences in equitability and abundance among years. There were also significant differences in equitability and abundance among years, and the year by site interaction was significant

for species richness, equitability, and abundance.

The highly disturbed sites had communities that were numerically dominated by *Dorymyrmex smithi*, which accounted for 97% of all ants in these sites.

Sweep Samples

We collected 1,295 ants (31 species) in our sweep net samples (Appendix B). There were significant differences among the three disturbance regimes in species richness ($F = 50.3$, $df = 2, 6$, $P < 0.05$) and equitability ($F = 8.9$, $df = 2, 6$, $P < 0.05$), but not in ant abundance ($F = 4.7$, $df = 2, 6$, $P > 0.05$). Both species richness and equitability were still significant after a sequential Bonferroni test ($P < 0.05$). The heavily disturbed sites had fewer species and a less equitable community (Student-Newman-Keuls, $P < 0.05$, Figure 3). There were also significant differences in species diversity and ant abundance among years.

Hand Sampling on Trees

We collected 2818 ants (15 species) from the lower trunks of oaks (Appendix C) and pines (Appendix D). The five most abundant species were *Dorymyrmex smithi*, *C. ashmeadi*, *Solenopsis invicta*, *Brachymyrmex musculus*, and *D. bureni*. Only one of these species, *C. ashmeadi* is predominantly arboreal. *Camponotus impressus*, the only other arboreal species we collected, was rare in our samples.

There were no significant differences among disturbance classes in S ($F = 0.159$, $df = 2, 6$, $P > 0.85$), arcsine E_H ($F = 0.111$, $df = 2, 6$, $P > 0.85$), and log N ($F = 0.844$, $df = 2, 6$, $P > 0.45$). There were significant differences in E_H among sites within disturbance classes ($F = 4.541$, $df = 6, 8.143$, $P < 0.05$) and between oaks and pines ($F = 5.369$, $df = 1, 8.989$, $P < 0.05$). Pines had a slightly greater average equitability of ant species. None of the effects, however, were significant once the experiment-wide error rate was adjusted for multiple comparisons (Sequential Bonferroni, $P > 0.05$).

There were no significant differences among disturbance classes ($F = 1.699$, $df = 2, 12$, $P > 0.20$) or tree types ($F = 0.082$, $df = 1, 12$, $P > 0.75$) in the abundance (log transform) of *C. ashmeadi*. The interaction between disturbance classes and tree types was also insignificant ($F = 1.022$, $df = 2, 12$, $P > 0.35$).

Total Species Diversity

Differences among disturbance classes were even more evident when we combined all species collected over four years of sampling, by all three sampling techniques. There were a total of 41 species in the lightly disturbed sites, and 41 species in the moderately disturbed sites. In contrast, there were only 31 species in the highly disturbed sites.

Discussion

Military training at Fort Benning clearly influences diversity

Table 3. Analysis of variance of species richness (*S*) in pitfall traps for the effects of disturbance class, site, and year.

Source of Variation	<i>DF</i>	<i>MS</i>	<i>F</i>
Among subjects			
Disturbance	2	115.1	18.2 ***
Site (Disturbance)	6	17.7	2.8 *
Sample (Site (Disturbance))	27	6.3	
Within subjects			
Year	2	12.3	2.5 ns
Year x Disturbance	4	0.56	0.12 ns
Year x Site (Disturbance)	12	9.63	1.98 *
Sample (Year x Site(Disturbance))	54	4.87	

Table 4. Analysis of variance of equitability (arcsine E_H) in pitfall traps for the effects of disturbance class, site and year.

Source of Variation	<i>DF</i>	<i>MS</i>	<i>F</i>
Among subjects			
Disturbance	2	2.93	27.34 ***
Site (Disturbance)	6	0.083	0.77 ns
Sample (Site (Disturbance))	27	0.107	
Within subjects			
Year	2	0.18	3.59 *
Year x Disturbance	4	0.35	0.72 ns
Year x Site (Disturbance)	12	0.13	2.65 **
Sample (Year x Site(Disturbance))	54	0.049	

Table 5. Analysis of variance of ant abundance (log *N*) in pitfall traps for the effects of disturbance class, site and year.

Source of Variation	<i>DF</i>	<i>MS</i>	<i>F</i>
Among subjects			
Disturbance	2	12.4	23.70 ***
Site (Disturbance)	6	0.35	0.67 ns
Sample (Site (Disturbance))	27	0.52	
Within subjects			
Year	2	1.72	8.52 **
Year x Disturbance	4	0.262	1.30 ns
Year x Site (Disturbance)	12	0.723	3.58 **
Sample (Year x Site(Disturbance))	54	0.202	

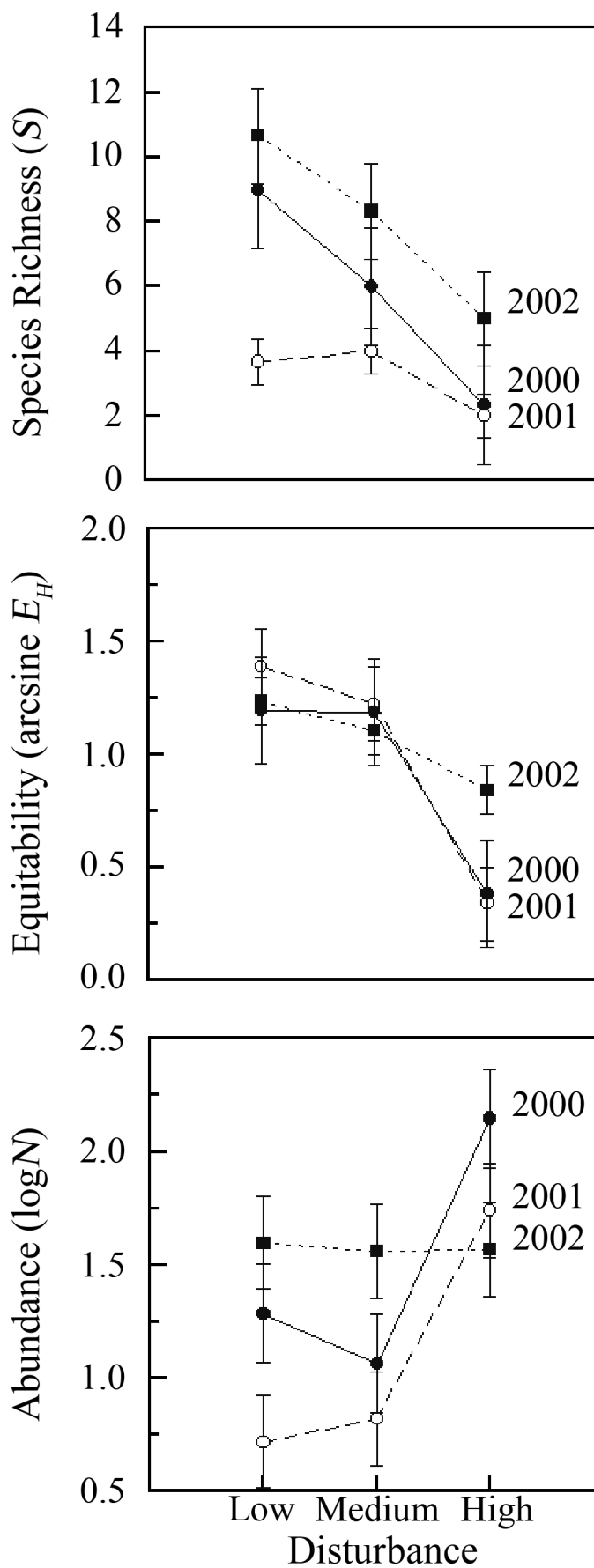
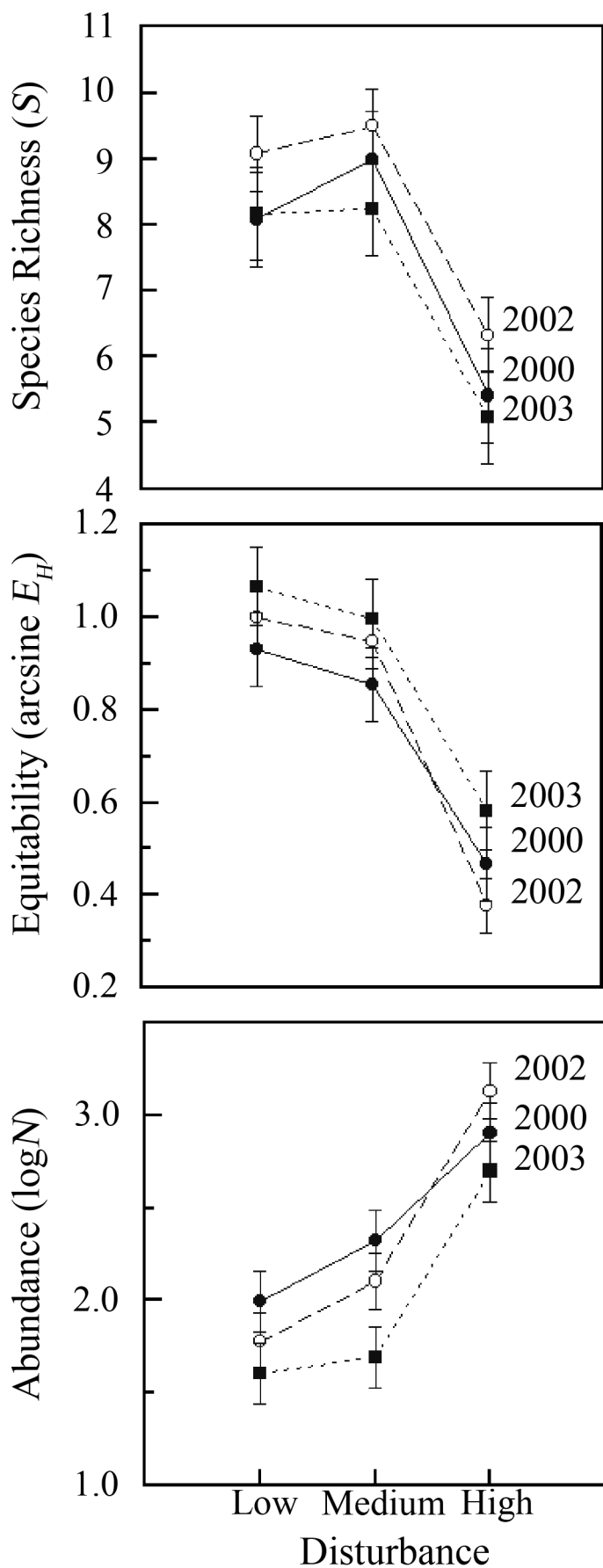


Figure 2. Effect of disturbance on species richness (S), equitability (E_H), and abundance ($\log N$) of ants in pitfall traps (2000, 2002, and 2003). Mean \pm standard error.

Figure 3. Effect of disturbance on species richness (S), equitability (E_H), and abundance ($\log N$) of ants in sweep net samples (2000, 2001, and 2002). Mean \pm standard error.

(species richness and equitability) and abundance of the ants collected in pitfall traps and sweep nets. There was no discernable influence, however, on the diversity and abundance of ants living or foraging on trees. These results are consistent with those of others who have studied ant communities in disturbed forest ecosystems. Majer (1983), Majer and Beeston (1996), and Andersen (1997a), for example, studied Australian eucalyptus forest disturbed by mining, agriculture, and urbanization. Bestelmeyer and Wiens (1996) studied ant communities disturbed by grazing in the Chaco of Argentina. In both Australia and Argentina, as in the sandhills of Georgia, disturbance reduced species diversity (both richness and equitability), benefited several species of Dolichoderines, and eliminated a variety of Myrmicines and cryptic species. In Argentina, species of Dolichoderinae, *Dorymyrmex* and *Forelius*, are common in highly disturbed sites (Bestelmeyer and Wiens 1996). Finally, increased abundance of ants in the disturbed sites is consistent with the thermal limitation hypothesis; cool temperatures limit the ability of ants to harvest resources (Kaspari et al. 2000).

Military training at Fort Benning creates open, warmer habitats having more compacted soils with a thinner A-horizon. These changes to the mixed pine/hardwoods forest differ from those caused by natural disturbances, such as wind, ice, fire, or insect and disease outbreaks. Wind and ice storms may remove trees, especially large ones, from the canopy, but they have little immediate effect on smaller trees, soils, woody debris, and under-story vegetation (Gresham et al. 1991; Matlack et al. 1993; Rebertus et al. 1997). Thus, they should have little effect on litter-dwelling ants at larger than gap scales. Moreover, fire in the sandhills is seldom hot enough to convert fire-adapted forest to grassland (Gibson et al. 1990); it removes woody shrubs, forbs, and fire-intolerant trees, but has little impact on older pines, especially longleaf pine (Glitzenstein et al. 1995; Hermann et al. 1998; Haywood et al. 2001). Moreover, fire-adapted shrubs and forbs re-sprout rapidly after a fire. Abrahamson (1984), for example, found that less than 2 years was necessary for recovery of soil chemistry and vegetation in Florida sandhills, pine scrub, and flatwoods forests. Fire has positive effects on some herbs, negative effects on others (Anderson and Menges 1997). Thus, fire alone removes habitat for litter-dwelling cryptic species, but at the same time doesn't create open, dry habitat favored by some ants.

The most abundant species in our heavily disturbed areas was *Dorymyrmex smithi*, a broadly-distributed Dolichoderine that is found from North Dakota to eastern Colorado and New Mexico, east through Texas to North Carolina and Florida (Snelling 1995). Although this species was widespread at Fort Benning, it was phenomenally abundant in disturbed areas. The three highest counts of any ant species in a single pitfall sample were all of *D. smithi*: 14,380 from H1, 10,535 from H2, and 9,480 from H3. These high numbers undoubtedly represent placement of pitfalls near colonies. Nevertheless, given our visual assessment of the density of *Dorymyrmex* colonies (they have distinctive conical mounds), it is likely that most clusters would be placed near colonies simply by chance.

A second species of *Dorymyrmex*, *D. bureni*, was more common in less disturbed sites. Nevertheless, densities there were much less than those of *D. smithi* at the disturbed sites. A third species, *D. grandulus*, was very rare. A

single specimen was found at L1, a site that had few *D. smithi*. We have since found additional specimens of *D. grandulus* elsewhere at Fort Benning.

The Dolichoderinae are most common in arid environments (Agosti et al. 2000). *D. smithi* forms large polycalic (several nests) colonies (Nickerson et al. 1975; Trager 1988), and the workers are particularly aggressive. According to Trager (1988), *D. smithi* occurs in the same disturbed habitats as *D. bureni*, such as "dunes, old fields, roadsides, lawns, pastures, and unpaved roads". *D. smithi* is a temporary social parasite of *D. bureni* (Buren et al. 1975, Trager 1988), so one might expect them to co-occur. At Fort Benning, however, the two species were negatively associated in our samples. *D. bureni* was more abundant in the less disturbed habitats, while *D. smithi* was more abundant in the most highly disturbed habitats. Nevertheless, we found numerous colonies of *D. bureni* on the lawns in the Fort Benning cantonment area. So it appears that *D. bureni* and *D. smithi* are both present in disturbed areas with different characteristics.

Other ants prevalent in the disturbed sites included *Solenopsis invicta*, *S. carolinensis*, *Pheidole bicarinata*, *P. crassicornis*, *Pogonomyrmex badius*, *Brachymyrmex musculus*, *Formica pallidifulva*, *Paratrechina arenivaga*, and *P. vividula*. In Michigan, *Pheidole bicarinata* is one of the few species to nest on the dunes of Lake Michigan (Talbot 1934). Likewise, *Pogonomyrmex badius* prefers open, exposed locations, and will move its nest if it is shaded (Carlson and Gentry 1973). *Formica pallidifulva* is an opportunist that prefers very warm temperatures (Talbot 1946). Two rarely sampled species, *Myrmecina americana* and *Pseudomyrmex pallidus*, were collected only in the disturbed sites. *Pseudomyrmex pallidus* nests in the stems of grasses (Van Pelt 1958). Seven species were never found in the heavily disturbed sites: *Hypoponera* sp. 1 and sp. 2, *Monomorium minimum*, *Temnothorax (Leptothorax) davisii*, *Aphaenogaster treatatae*, *Strumigenys louisianae*, and *Myrmica latifrons*.

Arboreal Ants

We found *C. ashmeadi* equally common on longleaf, shortleaf, and loblolly pines and oaks (several species). Johnson (1988) reported two color morphs (possibly two sibling species), a dark form prevalent on oaks and a bi-colored form prevalent on pines. We found these color morphs at Fort Benning, as well. We also observed that larger oaks and pines had more *C. ashmeadi* than smaller trees. According to Tschinkel (2002), larger trees support larger colonies of this species.

Ants are an important food for woodpeckers. The Red-cockaded Woodpecker, a federally endangered species, is the focus of management on military lands in the Southeast (Baker 1995; Cantrell et al. 1995; Dominy 1995; Hardesty et al. 1995). It eats more ants than any of the other seven woodpecker species in the Southeast, including the Northern Flicker, considered an ant specialist (McFarlane 1992). The arboreal ant, *C. ashmeadi*, is a major component of its diet (Hess and James 1998). Red-cockaded Woodpeckers prefer to forage on pines >30 cm dbh, especially during the breeding season (Bradshaw 1995).

C. ashmeadi density should be proportional to the density of large trees, because the numbers of *C. ashmeadi* on the few large pines and oaks in the disturbed areas were similar to those on

large trees in the lightly and moderately disturbed areas. Average densities of large trees declined from 2.2 trees per 3600 m² in the lightly disturbed sites, to 1.6 trees per 3600 m² in the moderately disturbed sites, and to 0.4 trees per 3600 m² in the heavily disturbed sites. Thus, *C. ashmeadi* populations in moderately disturbed areas should be reduced by 27%, while those in highly disturbed areas should be reduced by 82% (i.e. proportional to the reduction in large trees).

Exotic Species

Exotic ants can sometimes dominate disturbed habitats (McGlynn 1999; Agosti et al. 2000). *Solenopsis invicta*, the red imported fire ant, is a major pest in the southeastern United States; it sometimes reduces species diversity and abundance of native ants (Morrison 2002). Tschinkel (1988, 1993), for example, found *S. invicta* to be more common in disturbed habitats in northern Florida, where it displaced native ants. At Fort Benning, however, we found these generalizations to be only partially true. Although *S. invicta* was the most abundant ant in the pitfall traps at our lightly and moderately disturbed sites, it was only the second most abundant ant in our heavily disturbed sites. It was also the second most abundant ant overall, after *D. smithi*. The density of *S. invicta*, however, was not noticeably greater in our disturbed sites. Often, the samples with the greatest number of species also had the greatest number of *S. invicta*. Lubertazzi and Tschinkel (2003) also found that *S. invicta* tends to prefer the pine flatwoods in northern Florida dominated by herbaceous vegetation, such as wiregrass. Wiregrass dominance indicates a very frequent cycle of burning. Thus, the high fire frequency in all of our sites may contribute to the abundance of *S. invicta*. It is hard to say whether a three-year fire frequency constitutes additional disturbance or not.

Conclusion

Species richness, equitability, and abundance of ants in the southeastern Fall-Line Sandhills are all influenced by disturbance. Species richness and equitability are lower in highly disturbed habitats, but ant abundance is greater. Moderately and lightly disturbed sites are indistinguishable with respect to species richness and equitability. Moderately disturbed sites are intermediate with respect to abundance.

The density of arboreal ants (*C. ashmeadi*) on large pines and oaks is not influenced by disturbance. Nevertheless, because tree densities are less in disturbed sites, the density of *C. ashmeadi* per hectare is less.

Of the three sampling strategies, pitfall traps accounted for more species of ants than either sweep nets or searching of tree trunks. Sampling of ants with pitfall traps thus appears to be a promising approach for assessing and monitoring habitat disturbance caused by military training.

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Appendix A. Ant counts in pitfalls (2000-2003) by site.

Species	L1	L2	L3	M1	M2	M3	H1	H2	H3
<i>Aphaenogaster floridana</i> Smith	17	43	24	13	32	25	3	4	0
<i>Aphaenogaster rudis</i> complex	0	0	15	6	1	0	3	1	0
<i>Aphaenogaster treatae</i> Forel	7	8	23	8	9	4	0	0	0
<i>Brachymyrmex depilis</i> Emery	1	4	0	1	0	1	2	0	0
<i>Brachymyrmex musculus</i> Forel	39	55	9	8	3	1	11	50	23
<i>Camponotus caryae</i> (Fitch)	0	0	0	0	0	0	0	1	0
<i>Camponotus castaneus</i> (Latreille)	4	6	3	20	0	2	1	1	0
<i>Camponotus chromaiodes</i> Bolton	0	0	0	8	0	0	0	0	0
<i>Camponotus pennsylvanicus</i> (De Geer)	0	0	0	2	0	0	0	0	0
<i>Camponotus socius</i> Roger	3	9	21	0	7	6	8	9	0
<i>Crematogaster ashmeadi</i> Mayr	10	1	5	2	12	3	1	0	0
<i>Crematogaster lineolata</i> (Say)	21	3	15	17	57	7	4	0	0
<i>Crematogaster missouriensis</i> Mayr	14	7	17	23	38	33	4	4	0
<i>Dorymyrmex bureni</i> (Trager)	562	228	305	217	506	564	167	371	64
<i>Dorymyrmex smithi</i> Cole	289	14	13	3	0	4502	47998	25963	42723
<i>Forelius pruinosus</i> (Roger)	97	89	46	163	279	70	155	120	41
<i>Formica pallidifulva</i> Latrielle	24	49	66	26	31	49	14	95	12
<i>Hypoponera</i> sp. 1	1	1	3	1	1	0	0	0	0
<i>Hypoponera</i> sp. 2	0	0	1	0	0	3	0	0	0
<i>Monomorium viride</i> Brown	1	2	1	1	5	13	1	0	0
<i>Myrmecina americana</i> Emery	0	0	4	1	0	1	1	0	0
<i>Myrmica latifrons</i> Starcke	0	0	5	4	0	0	0	0	0
<i>Paratrechina arenivaga</i> (Wheeler)	6	5	15	41	2	13	25	16	4
<i>Paratrechina faisonensis</i> (Forel)	0	0	4	7	0	0	0	0	0
<i>Paratrechina parvula</i> (Mayr)	36	9	24	34	26	37	5	1	0
<i>Paratrechina vividula</i> (Nylander)	67	7	2	5	2	18	20	2	13
<i>Pheidole bicarinata</i> Mayr	0	3	2	0	0	0	7	31	31
<i>Pheidole crassicornis</i> Emery	172	221	271	315	234	123	21	18	4
<i>Pheidole davisii</i> Wheeler	2	0	0	0	0	0	0	0	0
<i>Pheidole dentata</i> Mayr	103	19	46	6	29	2	1	0	0
<i>Pheidole lamia</i> Wheeler	0	0	0	0	0	1	0	0	0
<i>Pheidole metallescens</i> Emery	0	2	0	1	75	0	9	10	0
<i>Pheidole morrisi</i> Forel	4	1	12	0	5	32	5	0	0
<i>Pheidole pilifera</i> (Roger)	0	57	1	4	226	0	0	0	0
<i>Pogonomyrmex badius</i> (Latreille)	0	0	0	0	3	0	58	3	0
<i>Prenolepis imparis</i> (Say)	18	1	106	40	1	310	0	8	36
<i>Solenopsis</i> nr. <i>carolinensis</i> Forel	34	8	45	41	32	38	14	5	31
<i>Solenopsis invicta</i> Buren	1265	196	117	2069	236	1086	605	600	724
<i>Strumigenys louisianae</i> Roger	2	0	0	0	0	0	0	0	0
<i>Temnothorax davisii</i> Wheeler	20	6	4	4	5	3	0	0	0
<i>Temnothorax pergandei</i> Emery	4	1	2	1	1	0	0	0	0
<i>Trachymyrmex septentrionalis</i> (McCook)	47	16	30	22	23	12	9	13	20

Appendix B. Counts of ants collected in sweeps (2000-2002) by site.

Species	L1	L2	L3	M1	M2	M3	H1	H2	H3
<i>Aphaenogaster floridana</i> Smith	0	1	0	0	0	0	0	0	0
<i>Aphaenogaster rudis</i> complex	0	0	0	0	1	0	0	0	0
<i>Brachymyrmex depilis</i> Emery	1	1	0	2	0	0	0	0	0
<i>Brachymyrmex musculus</i> Forel	30	27	4	5	1	11	1	11	5
<i>Camponotus castaneus</i> (Latreille)	0	0	1	0	0	0	2	0	0
<i>Camponotus pennsylvanicus</i> (De Geer)	1	0	0	0	0	0	0	0	0
<i>Crematogaster ashmeadi</i> Mayr	3	3	0	0	1	1	0	0	0
<i>Crematogaster lineolata</i> (Say)	22	3	4	16	1	1	3	0	1
<i>Dolichoderus mariae</i> Forel	0	0	0	0	4	0	0	0	0
<i>Dorymyrmex bureni</i> (Trager)	15	5	4	8	15	14	1	11	3
<i>Dorymyrmex grandulus</i> (Forel)	1	0	0	0	0	0	0	0	0
<i>Dorymyrmex smithi</i> Cole	1	3	0	0	4	1	226	62	491
<i>Forelius pruinosus</i> (Roger)	0	9	5	19	8	2	0	0	1
<i>Formica pallidifulva</i> Latreille	0	1	1	2	1	0	0	0	0
<i>Monomorium minimum</i> (Buckley)	33	0	0	0	0	0	0	0	0
<i>Paratrechina arenivaga</i> (Wheeler)	0	0	6	0	0	0	0	0	0
<i>Paratrechina faisonensis</i> (Forel)	1	0	0	4	0	0	0	0	0
<i>Paratrechina parvula</i> (Mayr)	8	5	1	8	14	1	0	0	0
<i>Pheidole bicarinata</i> Mayr	0	0	0	2	0	0	0	0	0
<i>Pheidole crassicornis</i> Emery	2	0	1	6	2	1	0	25	0
<i>Pheidole dentata</i> Mayr	2	0	0	0	0	0	0	0	0
<i>Pheidole pilifera</i> (Roger)	0	1	0	0	3	0	0	0	0
<i>Pogonomyrmex badius</i> (Latreille)	0	0	0	0	3	0	0	0	0
<i>Prenolepis imparis</i> (Say)	0	0	0	1	0	0	2	0	0
<i>Pseudomyrmex pallidus</i> (F. Smith)	0	0	0	0	0	0	1	0	0
<i>Solenopsis</i> nr. <i>carolinensis</i> Forel	1	0	0	0	0	0	0	0	0
<i>Solenopsis invicta</i> Buren	7	1	6	10	6	1	0	0	3
<i>Temnothorax curvispinosus</i> Mayr	0	0	0	1	0	0	0	0	0
<i>Temnothorax davisii</i> Wheeler	8	4	4	4	1	0	0	0	0
<i>Temnothorax pergandei</i> Emery	0	3	0	6	0	0	0	0	0
<i>Trachymyrmex septentrionalis</i> (McCook)	1	4	2	0	4	0	0	8	0

Appendix C. Counts of ant species collected on oaks (*Quercus* spp.) by site.

Species	L1	L2	L3	M1	M2	M3	H1	H2	H3
<i>Brachymyrmex musculus</i> Forel	11	1	0	5	10	0	5	34	0
<i>Camponotus castaneus</i> (Latreille)	0	0	0	3	1	0	0	0	2
<i>Camponotus impressus</i> (Roger)	0	2	0	0	0	0	1	0	0
<i>Crematogaster ashmeadi</i> Mayr	52	47	0	84	48	34	77	2	41
<i>Dorymyrmex bureni</i> (Trager)	2	0	1	1	0	35	1	0	0
<i>Dorymyrmex smithi</i> Cole	0	0	366	1	0	0	56	246	0
<i>Forelius pruinosus</i> (Roger)	0	7	0	7	0	0	0	0	0
<i>Formica pallidifulva</i> Latreille	0	1	0	1	0	0	0	0	0
<i>Paratrechina parvula</i> (Mayr)	4	0	0	0	0	0	0	0	0
<i>Paratrechina vividula</i> (Nylander)	2	1	0	0	0	0	0	0	0
<i>Pheidole dentata</i> Mayr	0	0	0	5	0	0	0	0	0
<i>Solenopsis</i> nr. <i>carolinensis</i> Forel	0	1	0	0	0	0	0	0	0
<i>Solenopsis invicta</i> Buren	90	44	0	2	73	0	2	41	8

Appendix D. Counts of ant species collected on pines (*Pinus* spp.) by site.

Species	L1	L2	L3	M1	M2	M3	H1	H2	H3
<i>Brachymyrmex musculus</i> Forel	32	54	0	30	38	0	36	79	0
<i>Crematogaster ashmeadi</i> Mayr	51	117	2	26	43	5	33	4	0
<i>Dorymyrmex bureni</i> (Trager)	2	11	0	69	16	0	27	7	0
<i>Dorymyrmex smithi</i> Cole	0	0	0	0	0	0	17	46	428
<i>Forelius pruinosus</i> (Roger)	0	0	0	4	0	0	0	46	0
<i>Paratrechina parvula</i> (Mayr)	0	0	0	9	0	0	0	0	0
<i>Paratrechina vividula</i> (Nylander)	1	0	0	0	0	0	1	0	0
<i>Pheidole crassicornis</i> Emery	0	0	0	0	0	1	0	0	0
<i>Solenopsis invicta</i> Buren	7	1	0	3	8	0	86	21	0
<i>Trachymyrmex septentrionalis</i> (McCook)	0	0	1	1	0	0	0	0	0