Habitat Associations of Ant Species (Hymenoptera: Formicidae) in a Heterogeneous Mississippi Landscape

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ABSTRACT Community assembly and the factors that influence it have long been a topic of interest to ecologists, but theory has yet to produce unequivocal evidence that communities assemble in predictable ways. The goal of this study was to document the relationship between ant communities and environmental variation between four habitat types. To accomplish this, ant communities and 16 environmental variables were sampled across four different habitat types in the Black Belt Prairie and Flatwoods regions in Mississippi. Furthermore, ant species were placed into functional groups for an analysis of the relationship between the assembly of ecological communities and variation in ecosystem function. A total of 20,916 ants representing 68 species was collected across the four habitat types. Nonmetric multidimensional scaling and analysis of covariance analyses both revealed three distinct ant communities, which can be characterized by habitat type: pasture, prairie, and woodland. Principle components analysis (PCA) simplified the 16 environmental variables into four principle components that explained 78% of the variation among sites. Results of multiple regression using the four PCA axes as predictor variables suggest that regional variation in soil structure, land cover type, and the presence of grazing have had major influences on ant community composition. Variation in flora and habitat architecture had smaller but significant effects on ant species diversity and functional group composition. Our results imply that restoration of native ant communities in disturbed habitats must consider how current disturbance regimens likely interact with the presence of *Solenopsis* to lower ant biodiversity.

KEY WORDS Black Belt Prairie, ecological assembly, Formicidae, *Solenopsis,* Mississippi

Associations between ant species (Hymenoptera: Formicidae) and particular habitat types are poorly know for many ecoregions. This may be somewhat surprising given that the ant fauna of many states in the United States is relatively well known. For example, the ant fauna of Mississippi was documented by Marion Smith in the 1920s through the early 1930s and by the more recent surveys of the Mississippi Entomological Museum (Smith 1924a, b, c, 1927, 1928a, b, 1931, 1932, MacGown et al. 2005, MacGown and Brown 2006). However, with the exception of MacGown and Brown (2006), little work has been done to examine the ant community of specific habitat types within the state, nor have there been many studies into what environmental factors are most influential in differentiating ant community composition between habitats.

Ants may be among the most promising groups of animals for inclusion in community-based studies because of their contributions to ecosystem function. They directly and indirectly affect faunal and floral groups by predation, scavenging, tending homopterans, protecting certain plants, dispersing seeds, and also aiding in nutrient and soil turnover (Wheeler 1910, Hölldobler and Wilson 1990, Agosti et al. 2000, Gorb and Gorb 2003). Ants also are of interest because of the putative deleterious effects caused by nonnative species, especially the imported fire ants, *Solenopsis invicta* Buren, *S. richteri* Forel, and their hybrid *S. invicta* × *richteri,* which negatively affect human endeavors and reduce biodiversity in the communities they invade (Porter and Savignano 1990, Morris and Steigman 1991, Vinson 1997).

Ants are an important taxon for comparing habitat diversity and monitoring environmental changes because numerous species have habitat preferences and respond quickly to disturbances to their environment (Andersen 1990, Alsonso 2000, Kaspari and Majer 2000). Indeed, ants have been used extensively for several decades in Australia as bioindicators of habitat change (Greenslade and Greenslade 1984, Andersen 1990, 1997, Boulton et al. 2005, Ratchford et al. 2005). The use of ants in a similar manner has gained in popularity recently in North America, with several studies investigating how the relationships between various characteristics of a habitat, such as abiotic factors, structure of the plant community, and soil properties, affect the local ant assemblage (Herbers

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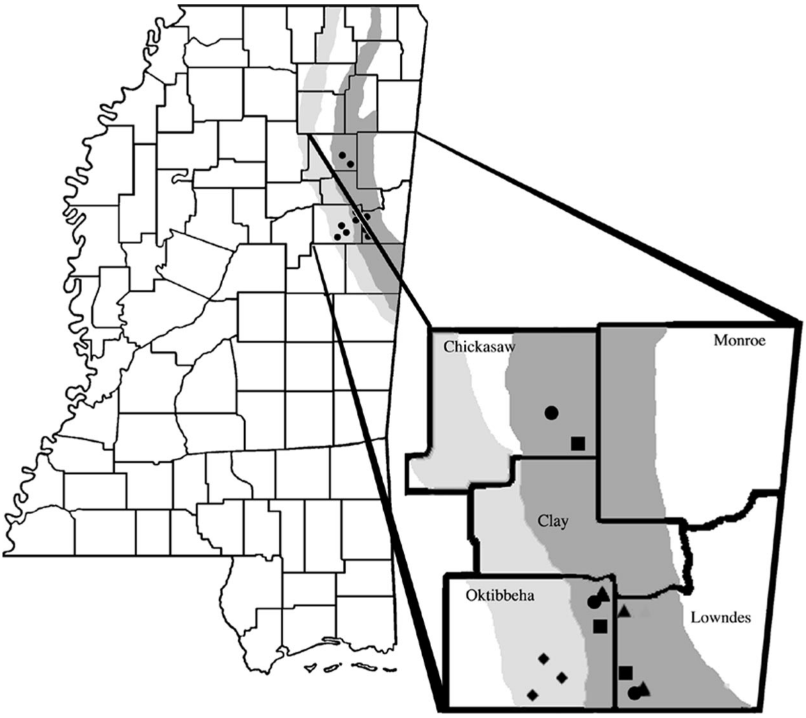

Fig. 1. Map of Mississippi showing the Black Belt (dark gray) and Flatwoods (light gray) and position of study sites. ■, pasture; ●, prairie; ▲, oak hickory; ◆, Flatwoods.

1989, Gotelli and Arnett 2000, Wang et al. 2001, Gotelli and Ellison 2002). Alternatively, disturbances such as fire tend to have a positive effect on the some ant guilds while having a negative effect on others (Izhaki et al. 2003). Learning more about ant ecology of the various habitats in Mississippi is important not only to provide a better understanding of the overall ant fauna of the state but also to guide current management and future conservation/restoration projects in those systems. Mississippi contains many notable habitats, including some of North America's most threatened habitats such as the Black Belt Prairie. Unfortunately, government-supported conservation of endangered habitats has had a low priority in Mississippi, making present community-based studies important.

This study documented the relationship between ant community composition and habitat by examining the ant communities and environmental variables across four habitat types and two physiographic regions in Mississippi to determine whether the ant community of these four habitats differ, and if so, to identify what environmental factors are important in determining ant community composition. The four habitat types include: prairie, actively grazed pasture that was historically prairie, and oak-hickory forests in the Black Belt physiographic region and pine-oak forests in the Flatwoods physiographic region. A third goal of this research was to study any potential relationship between habitats and imported fire ant and native ant populations. Understanding the ant fauna of the various habitats of this region and the factors that influence them should provide information for management and restoration purposes and possibly control of imported fire ants.

Materials and Methods

Study System. We conducted our study within the Black Belt and Flatwoods physiographic region of northeastern Mississippi (Fig. 1). The Black Belt Prairie physiographic region extends from McNairy County, TN, in an arc south through eastern Mississippi to Russell Co., AL. Instead of being a continuous swath of open land, the Black Belt historically represented a heterogeneous landscape of prairies and several types of forest (Barone 2005). The presence of the prairies is caused, at least in part, by distinctive calcareous loamy soils that have a pH in the 7.5–8.5 range. Floristic surveys of the prairies have shown a distinct grassland community similar to that of the Great Plains with several rare or critically imperiled plant species present (Leidolf and McDaniel 1998, Barone and Hill 2007). Most of the original Black Belt prairie has been lost to agriculture, development, and the incursion of eastern red cedar, *Juniperus virginiana* L. (Cupressaceae), making it among the most endangered communities within the state and possibly the southeast (Brown 2003).

The Black Belt's fertile soils made it one of the most agriculturally important areas of the Mississippi. The native grasslands of the region that once provided forage for the livestock of early settlers have been

Table 1. Location and dominant vegetation present at each of the 12 sites used in this study[a]

Site name	Habitat type	County	Latitude and longitude	Dominant vegetation
Crawford	Prairie	Lowndes	33°18′4″ N 88°36′46″ W	C4 grasses
Osborn	Prairie	Oktibbeha	33°30′21″ N 88°44′09″ W	C4 grasses
Tombigbee National Forest	Prairie	Chickasaw	33°55′38″ N 88°51′17″ W	C4 grasses
Crawford	Pasture	Lowndes	33°18“17″ N 88°37′41″ W	C3 grasses
Starkville	Pasture	Oktibbeha	33°25′43″ N 88°44′06 W	C3 grasses
Trebloc	Pasture	Chickasaw	33°49′51″ N 88°48′32″ W	C3 grasses
Crawford	Oak-Hickory	Lowndes	33°17′57″ N 88°36′30″ W	Deciduous trees
Osborn	Oak-Hickory	Oktibbeha	33°30′51″ N 88°43′51″ W	Deciduous trees/cedar
Hwy82 × Hwy 45A	Oak Hickory	Lowndes	33°29′06″ N 88°39′39″ W	Deciduous trees
Watkin's Forest	Flatwoods	Oktibbeha	33°22′48″ N 88°49′46″ W	Pine/deciduous trees
Hankin's Forest	Flatwoods	Oktibbeha	33°20′38″ N 88°49′00″ W	Pine/deciduous trees
Noxubee N.W.R.	Flatwoods	Oktibbeha	33°20′45″ N 88°54′32″ W	Pine/deciduous trees

[a] Ants were sampled from three plots within each study site.

replaced with pastures of non-native species and various row crops, especially corn, cotton, and soybean. Today, pastures are widespread in the area, contain few plant species relative to natural systems, and are often planted in non-native grasses The oak-hickory forests of the Black Belt occur on the elevated areas of reddish, acidic soil that dot the prairie surface like islands (Lowe 1921). Kaye (1955) considered these soils, which are situated atop the Selma chalk, to be Pleistocene aeolian deposits of loess. These forests are dominated by *Quercus marilandica* (Muench.), *Q. velutina* (Lam.), *Q. stellata* (Wangenh.) (Fagaceae), *Carya ovata* (Mill.), *C. tomentosa* (Poir.) (Juglandaceae), and *J. virginiana.* Finally, the Flatwoods physiographic region lies immediately west of the Black Belt and Pontotoc Ridge regions. This region is formed on heavy clay soils with poor drainage that supports a pine-oak community differing significantly in floristic composition from the forests of the Black Belt. *Pinus taeda* L. (Pinaceae), *Quercus falcata* Michaux, *Q. stellata* Wang., *Liquidambar styraciflua* L.(Hamamelidaceae), and *Acer rubrum* L. (Aceraceae) are the dominant tree species forming this forest system.

Selection of Study Sites. Three sites were chosen for ant community sampling in each of the four habitat types: prairie, actively grazed pasture, oak-hickory forest, and pine-oak flatwoods (see Table 1 for site descriptions). Prairie sites were selected based on plant composition, size of the remnant, lack of recent disturbance, and cooperation of the landowner/manager. To minimize differences in basic soil composition, weather, and other unrecognized variables, pasture sites were selected that were in close proximity to the prairie remnants and were in areas that historically were covered by prairie (Barone 2005). Selected pastures were also actively grazed in a manner typical of the region, (e.g., planted in non-native grasses and averaging approximately one head of cattle per two acres). Forested sites were selected that occurred within near to the pasture and prairie habitats (Fig. 1). Three circular plots measuring 25 m in diameter were established at each of the three sites in all four habitat types. Thus, a total of 9 plots were established in each habitat type, and 36 plots were established in all.

Sampling Ant Communities. Because ants display a wide array of habits and behaviors, we sampled with a variety of techniques in each plot including pitfall traps, litter sampling, baiting, and active searching. Sampling occurred from June to October 2003 and from April to December 2004. Pitfall traps were operated in each of the 36 plots for 7-d periods on alternating weeks during the sampling period of 2003. Each plot had six pitfall traps that were grouped into three sets of two with a sheet metal barrier measuring 45 by 7.5 cm between the two traps to deflect any passing ants. Each trap consisted of a plastic cup with an internal diameter of 10.5 cm and a depth of 7.5 cm. These cups were placed so that their tops were flush with the ground surface, and cups were filled halfway with a solution of 50% propylene glycol and 50% ethanol (70%). Each cup was covered with a hexagonal, sheet metal cover, elevated by three bent corners, to prevent entry of rain and evaporation of preservatives in traps exposed to sunlight. The three sets of traps were arranged in an equilateral triangle with 10 m between each set. Each site had 18 total pitfalls, resulting in 54 pitfalls per habitat and 216 total traps over the entire study area. Samples of litter and soil were collected from each forest plot to fill a 3.75-liter plastic bag once a month in 2003 and twice a month in 2004. For extraction of ants, these samples were placed in a Berlese funnel under a 40-W light bulb until the litter was dry, which usually required 3–5 d. General collecting was performed within each plot for 30 min twice a month during the sampling periods in 2003 and 2004, with all individuals observed being collected. This collecting consisted of hand sifting of soil, grass duff, and leaf litter, active searching, and baiting. Searching consisted of looking for nests and foragers on the open ground, under rocks and logs, and inside rotten logs, stems, and other plant parts. Tuna fish (StarKist chunk light in water, Del Monte Foods, San Francisco, CA), cookies (Keebler Sandies Pecan Shortbread, Kellogg Co., Battle Creek, MI), and peanut butter (various brands) were used as baits at each site. These three baits were typically rotated per collection date and placed in three locations within the plot on the bare ground, on the trunks of trees, or on both, and all individuals present at the bait were collected after 30 min. Ant taxonomy is based on Bolton (2003), except *Polyergus,* which follows Smith (1947), and *Pheidole,* which follows Wilson (2003). Voucher specimens were deposited in the Mississippi Entomological Museum (MEM).

Measuring Environmental Variables. We measured the following local environmental variables within each sampling plot: plant species richness and diversity, diameter at breast height (DBH) of trees, percent canopy cover, herbaceous/shrubby vegetation height, the amount of coarse woody debris (CWD) on the ground, and soil attributes. Percent grass, C_3/C_4 graminoid ratio, and herbaceous richness were calculated from plant richness and diversity measures that were sampled using eight 0.25-m^2 wire frames that were randomly placed within the plots. Every plant within each frame was identified and counted during June and July 2004. DBH values were used to calculate stand basal area (m^2/ha) for all plots. Percent canopy cover was measured by taking the mean of five random densitometer measurements within the plots. Coarse woody debris was measured by taking the diameter at both ends and the length of all downed woody objects. These figures were used to calculate the volume of a frustum cone and expressed as cubic meters per hectare. Regional variables were confined to land cover type and edaphic parameters that were measured by taking a core of soil from the first 3 cm from several areas within each plot. These samples were analyzed at the Mississippi State University Extension Service's soil testing laboratory for the follow attributes: percent organic matter (OM), pH, kilograms per hectare of P, K, Ca, Mg, Zn, S, and Na, milliquivalents per 100 g of H, K, Ca, and Mg, percent clay, percent sand, and percent silt.

Data Analysis. Studies of community assembly are often limited by incomplete sampling of the regional species pool (Summerville et al. 2006). To ensure that the regional species pool of ants among the four habitat types and ants in each habitat type were sampled efficiently, we generated a species accumulation curve using EstimateS (Colwell 2005) and calculated an incidence-based coverage estimator (ICE) to quantify the potential number of unsampled species. EstimateS derives a species accumulation curve based on an average of a series of 1,000 randomizations of the species by sites data matrix (Colwell 2005). This randomization allows for a species accumulation curve that is independent of the order in which the samples were added into the analysis.

We used an analysis of covariance (ANCOVA) (PROC GLM; SAS Institute 2003) model to test the hypothesis that ant species richness varied among the four habitat types. Because species richness is a biased estimator of diversity when the number of individuals collected among sites varies, we considered ant abundance within each site as a covariate. To meet assumptions of normality, ant abundance was log-transformed before analyses (Krebs 1999). Thus, our ANCOVA model treated habitat type as a categorical fixed effect ($df = 3$) and log-abundance as a random effect ($df = 1$). In addition, to understand how differences in ant species richness related to differences in community structure, we used nonmetric multidimensional scaling (NMDS) to assess how ant species composition differed among the 36 sites. A full description of NMDS is given in McCune and Grace (1999), but briefly, NMDS differs from other commonly used ordination techniques in that NMDS differentiates among sampling units by ranking them according to their pairwise dissimilarity. We performed the NMDS ordination with PC-ORD (version 4; MJM Software Design, Glendon Beach, OR). Ant community data consisted of log-transformed species abundance for each site. We used the Bray-Curtis statistic as the measure of ordination distance among ant communities because it is one of the most robust statistics for multivariate analysis, and it is affected little by large numbers of rare species (Krebs 1999). In addition, we followed the recommendation of McCune and Grace (1999) and used multiple runs of the NMDS algorithm with our real data (100 total runs) to avoid local stress minima, a problem that prevents the ordination from converging on the lowest possible stress value. We used 1,000 Monte Carlo simulation runs to evaluate the significance of our final two ordination axes.

Finally, we used a two-step analysis approach to determine how local and regional factors interacted to produce ant communities. First, we used principle components analysis (PCA) to identify combinations of measured environmental variables that were highly intercorrelated (Graham 2003). The PCA was performed using SAS 9.1 (PROC PRINCOMP; SAS Institute 2003) and a total of 16 variables from the vegetation and soil sampling (Table 1). Because the units of measurement for these variables differed considerably, the correlation matrix among variables was used to generate PCA scores rather than their covariance matrix (Philippi 1993). One limitation of PCA is that ecological interpretation of the principal components may be difficult, so we chose a 0.35 minimum loading coefficient as a requirement before a given environmental variable was considered to significantly load on a PCA axis (after Summerville et al. 2005).

To test whether the number of species found within a site was predicted by combinations of environmental variables, we used multiple regression analysis (SAS PROC REG) with the scores of the orthogonal principal components as predictor variables (Graham 2003, Summerville et al. 2005). Only PCA axes with an eigenvalue ≥ 1.0 were included in the multiple regression analysis because they explained at least 10% of the variance among sites (Philippi 1993). Regressions were performed using total species richness and total ant abundance as response variables. We also created multiple regression models with number of individuals within functional groups as response variables to link differences in the community structure of ants to ecological function. Assignment of a species to a functional group was based on the classification system proposed by Andersen (1997) for Australia and Izhaki et al. (2003) for Florida pine savannas. Modifications were made to this system based on observations made

Table 2. Functional groups with assigned ant species collected in all habitats

Cold climate
Prenolepis imparis (Say)
Stenamma meridionale Smith

Cryptic
Amblyopone pallipes (Haldeman)
Discothyrea testacea Roger
Hypoponera inexorata (Wheeler)
Hypoponera opaciceps (Mayr)
Hypoponera opacior (Forel)
Ponera exotica Smith
Ponera pennsylvanica Buckley
Proceratium pergandei (Emery)
Pyramica clypeata (Roger)
Pyramica creightoni (Smith)
Pyramica dietrichi (Smith)
Pyramica missouriensis (Smith)
Pyramica ohioensis (Kennedy & Schramm)
Pyramica ornata (Mayr)
Pyramica pulchella (Emery)
Pyramica rostrata (Emery)
Pyramica talpa (Weber)
Strumigenys louisianae Roger

Dominant Dolichoderinae
Forelius mccooki (McCook)
Tapinoma sessile (Say)

Generalized Myrmicinae
Aphaenogaster carolinensis Wheeler
Aphaenogaster fulva Roger
Aphaenogaster lamellidens Mayr
Crematogaster ashmeadi Mayr
Crematogaster lineolata (Say)
Crematogaster minutissima Mayr
Crematogaster missuriensis Emery
Crematogaster pilosa Emery
Monomorium min. (Buckley)
Pheidole bicarinata Mayr
Pheidole dentata Mayr
Pheidole dentigula Smith
Pheidole tysoni Forel
Solenopsis invicta x *richteri*
Solenopsis molesta (Say)
Solenopsis richteri Forel

Subordinate Camponotini
Camponotus americanus Mayr
Camponotus castaneus (Latrielle)
Camponotus chromaiodes Bolton
Camponotus decipiens Emery
Camponotus impressus (Roger)
Camponotus mississippiensis Smith
Camponotus pennsylvanicus (DeGeer)
Camponotus snellingi Emery
Camponotus subbarbatus Emery

Opportunists
Pseudomyrmex pallidus (Smith)
Myrmica pinetorum Wheeler
Myrmica punctiventris Roger
Aphaenogaster flemingi Smith
Aphaenogaster treatae Forel
Pheidole pilifera (Roger)
Temnothorax curvispinosus Mayr
Temnothorax schaumii Roger
Temnothorax pergandei Emery
Myrmecina americana Emery
Trachymyrmex septentrionalis (McCook)
Lasius alienus (Foerster)
Lasius umbratus (Nylander)
Paratrechina arenivaga (Wheeler)
Paratrechina faisonensis (Forel)
Paratrechina vividula (Nylander)
Formica pallidefulva Latreille
Formica dolosa Wheeler
Formica subsericea Say
Polyergus lucidus longicornis Smith
Polyergus lucidus montivagus Wheeler

during this study and information from the literature to make it applicable to the study region (Table 2). Ants collected during this study were placed into the following functional groups: cold climate (species active only during the cooler seasons), cryptic (minute species that live mostly in the litter, rotting logs, or soil), dominant Dolichoderinae (aggressive and dominant species), generalized Myrmicinae (species that are found in many type habitats and defend resources by recruitment), opportunists (unspecialized, poorly competitive species), and subordinate Camponotini (submissive to dominant Dolichoderinae and foraging primarily at night).

Results

A total of 20,916 ants representing 68 species including the hybrid imported fire ant, *Solenopsis invicta* × *richteri*, were collected. *Solenopsis invicta* × *richteri* was the most common species (4,319 individuals), and when combined with the black imported fire ant, *S. richteri* (Forel), these introduced fire ants totaled 5,270 individuals, almost 2.5 times as many as the next most commonly collected species, *Crematogaster lineolata* (Say) (2,057). Ten species made up 75% of the total number of individuals collected. Therefore, the ant fauna of these regions in Mississippi seemed to be characterized by a small number of frequently sampled species that are habitat generalists and a large number of infrequently sampled species. For example, 14 ant species were restricted to single habitats and were represented by <6 individuals. The most species-rich functional group was the opportunists, with 21 species followed by cryptic (18 spp.), generalized Myrmicinae (16 spp.), subordinate Camponotini (9 spp.), cold climate specialists (2 spp.), and dominant Dolichoderinae (2 spp.). However, in terms of dominance of individuals, the generalized Myrmicinae ranked first with 14,698 individuals, followed by the opportunists (3,041individuals), dominant Dolichoderinae (1,164 individuals), cryptic species (1,008 individuals), subordinate Camponotini (780 individuals), and cold climate specialists (225 individuals).

The regional species accumulation curve showed considerable evidence of leveling off, and the ICE diversity estimator predicted that 70.14 total species were in the regional species pool among the four habitats. Because we actually sampled 68 species, our sampling efficiency was ≈97%. Species accumulation curves for the individual habitats showed evidence of leveling off with a lower but broadly similar level of sampling efficiency among all four types (prairie = 88%, pasture = 86%, oak-hickory = 93%, and Flatwoods = 89%; see Fig. 2). The ANCOVA comparisons of ant species richness across the four habitat types detected significant differences among the habitat types (Table 3; Fig. 3), with both forest types generally possessing more diverse ant communities ($F_{3,31} = 78.13; P \leq 0.0001$). Mean species richness within forest types was ≈25 species compared with 17.1 in prairies and 5.2 in pastures. Species richness, however, was also a function of the log-abundance of ants collected within each site ($F_{1,31} = 5.05; P = 0.032$). A marginally greater number of species were encountered when a larger number of individuals were sampled, but the biggest contribution to differences in abundance of ants among habitat types was *Solenopsis* spp. The NMDS ordination revealed three distinct ant communities based on species composition from the four habitat types (Fig. 4; final stress, 12.16; $P \leq 0.001$ for each axis). Pasture and prairie grouped independent of each other, whereas the two forest types were closely clustered in ordination space. The pasture sites

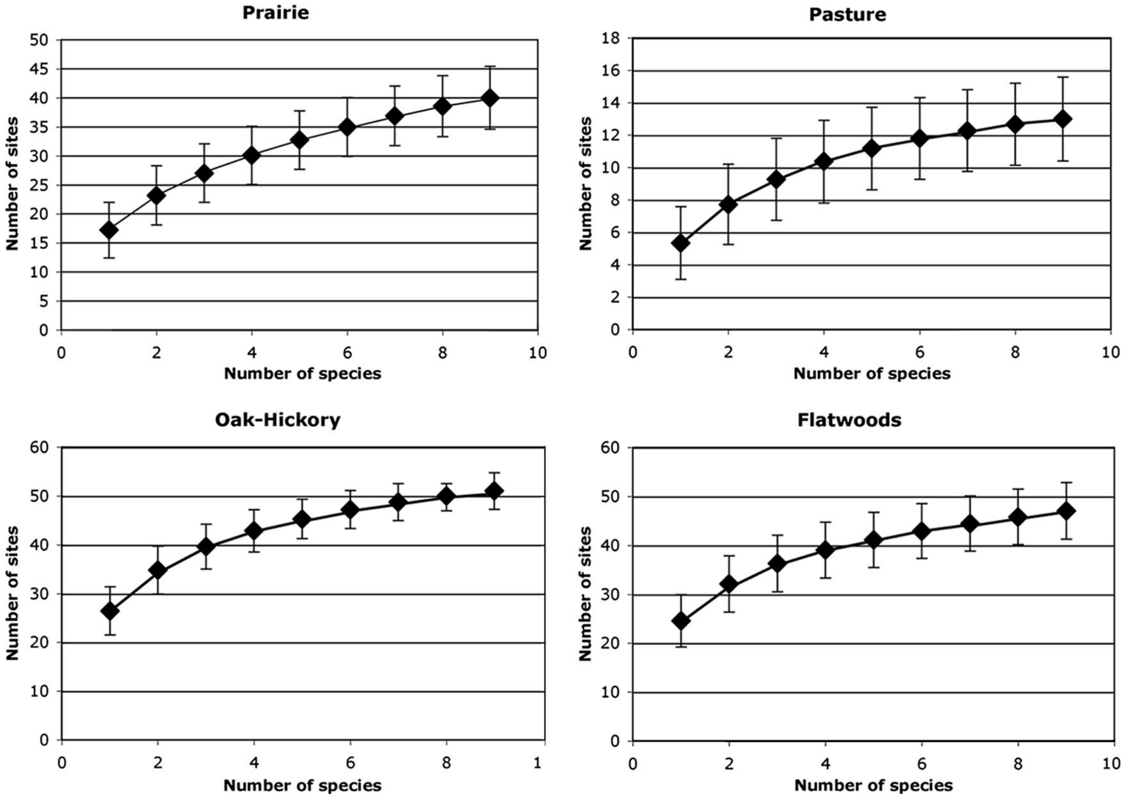

Fig. 2. Species-accumulation curve from the four habitat types based on an average of series of 1,000 randomizations of the species data. Error bars are ±SD based on 1,000 randomizations of the observed species × sites matrix.

possessed considerable variability, with sites possessing greater populations of *S. richteri* grouping separately from sites dominated by the hybrid fire ant *S. richteri* × *invicta.* A post hoc multiresponse permutation procedure (MRPP) test determined that Black Belt prairies, grazed pastures, and forests supported discrete groups of ants (observed $\delta = 0.41$, $A = 0.04$, $P = 0.0001$), but there was no significant difference between forest types ($P > 0.10$). Thus, the results of the ANCOVA analysis and the NMDS ordination were broadly congruent: forested sites within the Black Belt and Flatwoods regions possessed high diversity but broadly overlapping ant communities, whereas grassland systems in the Black Belt were greatly differentiated based on land use (pasture versus prairie) and identity of the dominant taxa (*S. richteri* versus *S. richteri* × *invicta*). Finally, conversion of Black Belt to managed pasture habitat was correlated with a significant reduction in ant species richness and abundance.

The PCA partitioned the 12 environmental variables into seven axes, of which only four possessed eigenvalues ≥1 (Table 4). These four principal components axes combined to explain 78% of the variance in environmental variables among the four habitat types. All of the environmental variables except several aspects of soil chemistry had a significant effect on the variation between the four habitat types. In general, the first PCA axis distinguished among habitat types based on the effects of regional environmental variation. Sites that loaded positively on the first PCA axis had a high soil pH, Ca^{2+} content, and herbaceous

Table 3. Results of ANCOVA models testing whether ant species richness was affected by habitat type (four levels: pasture, prairie, oak-hickory, and Flatwoods) or the no. of individuals collected (log ant abundance)

Source of variation	df	MS	*F*	*P*
Habitat type	3	815.79	78.13	0.0001
Log ant abundance	1	52.76	5.05	0.0318
Error	31	10.44		

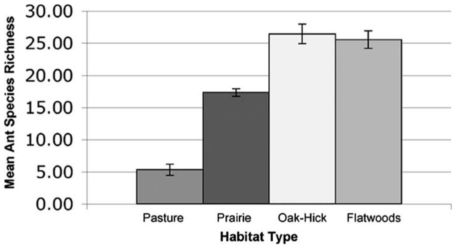

Fig. 3. Mean ants species richness across the four focus habitat types.

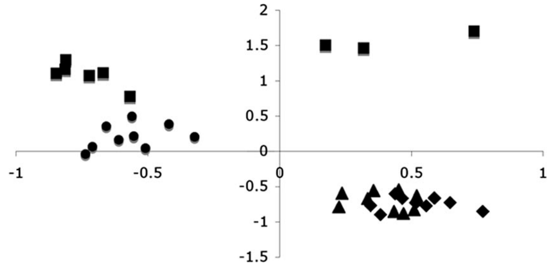

Fig. 4. NMS ordination of the focus habitat types. ■, pasture; ●, prairie; ▲, oak-hickory; ◆, Flatwoods. Both x- and y-axes were significant ($P < 0.001$).

richness, with low canopy cover and basal area. Therefore, this axis essentially divided the four habitats into two broad categories: open and forested (Fig. 5). Alternatively, principal components 2–4 each teased out differences among habitat types based on increasingly more specific local factors. For example, sites that loaded positively on the second PCA axis (PCA 2) had a high percent soil organic matter content, a high percent C_3 graminoid composition, and low percent sand in the soil. This axis was most important in differentiating among grassland habitat types, with pasture sites loading positively and prairie sites loading negatively. On the third PCA axis (PCA 3), sites that loaded positively had high herbaceous height, high C_3 diversity, and a low percent soil organic matter; this axis defined the Flatwoods forest stands from all other habitat types. Finally, sites loading positively on the fourth PCA axis (PCA 4) had a high cover of coarse woody debris and uniformly low graminoid cover—characteristics that defined the oak-hickory sites.

Multiple regression models using the first four principal components revealed that total ant richness was significantly predicted by the first, second, and fourth principle components ($R^2 = 0.72$, model $F_{4,30} = 19.64$, $P \leq 0.001$). Interestingly, the parameter estimates for the first two principle components were negative, indicating that sites with high soil pH, low values of canopy cover, and negligible basal area (prairie and pasture) supported significantly lower numbers of ant species compared sites with acidic soil, high values of canopy cover and basal area, and more coarse woody debris (forested sites; Table 5). Thus, the "habitat effect" we observed from the ANCOVA seemed to be principally driven by variation three variables (soil pH and land cover type and cover of coarse woody debris within oak-hickory forests).

Table 4. Results of PCA for 12 environmental variables measured across 36 plots from pasture, prairie, oak-hickory forest, and Flatwoods

Environmental variable	Principal component axis			
	1	2	3	4
Percent OM	0.132	**0.448**	**−0.384**	0.327
Herbaceous height (cm)	0.175	−0.283	**0.467**	0.328
Percent grass	0.200	0.255	**0.432**	**−0.517**
CWD (m^2/ha)	−0.131	0.101	0.267	**0.493**
pH	**0.448**	−0.072	0.083	0.032
C3/C4 graminoid ratio	−0.137	**0.389**	**0.511**	0.002
Percent canopy cover	**−0.427**	0.127	−0.077	0.197
P (kg/ha)	0.237	0.304	−0.183	−0.247
Basal area (m^2/ha)	**−0.385**	0.011	0.183	0.048
Ca (milliquivalents/100 g)	**0.374**	0.242	0.133	0.288
Herbaceous richness	**0.381**	−0.241	−0.101	0.263
Percent sand	−0.050	**−0.512**	0.106	−0.143
Eigenvalue	4.373	2.476	1.364	1.166
Cumulative variance explained by axis	0.364	0.571	0.684	0.782

Bold type indicates significant factor loadings.

Abundance of ants within several functional groups was most consistently influenced by variation in the first principal component, with other PCA factors affecting only certain groups of ants (Table 5). This effect was most likely observed because some functional groups prefer to nest and forage in shaded, structurally complex habitats with abundant litter (cold climate, cryptic species, and subordinate Camponotini), whereas other species seemed restricted to more open areas (dominant Dolichoderinae, *Solenopsis* spp.). Cold climate specialists contained the least number of individuals captured, which may be attributed in part to a lack of sampling during winter months, and their numbers were not significantly different across all four habitat types (model $R^2 = 0.22$; $P = 0.09$; Table 1). Species within the cryptic functional group also attained higher abundance in structurally complex habitats with low herbaceous species richness, especially those having higher coarse woody debris content and fewer grasses (e.g., significant effects of PCA1 and PCA4; Table 4). Abundance of dominant Dolichoderinae was predicted by a positive effect of PCA1, indicating a preference for open areas, and a negative effect of PCA2, suggesting that they are also susceptible to grazing disturbance (Table 5). Abundance of the opportunist functional group was predicted by the first two principal components, but each effect was negative (Table 4). This suggests that these species avoid areas with C_3 grasses (e.g., grazed sites) and prefer sites with calcium-deficient soils and higher canopy cover of larger trees. Analysis of the significant principle component effects indicated that subordinate Camponotini were most abundant in the two forest types and occurred marginally less than in prairie and significantly less in pastures. A significant negative effect of PCA 1 suggested that these species occurred in more forested areas, whereas the negative effect of PCA 3 indicated higher abundances in habitats with low herbaceous height, high soil organic matter, and higher C_3 graminoid content (Table 5). The generalized Myrmicinae were not significantly influenced by any of the measured environmental variables. To further study what variables influence imported fire ant abundance (*Solenopsis* spp.), they were analyzed separately from the generalized Myrmicinae. We determined that imported fire ants were most abundant in pastures with significantly lower numbers found in prairie remnants and the two forest types ($F_{3,31} = 42.31$; $P \leq 0.0001$). Alternatively, generalized Myrmicinae minus fire ants were most

Table 5. Multiple regression models using the first four principal component axes, total species richness, and functional group abundance

Dependent variable	Predictor variable	df	R^2	F	P	Parameter estimate (SE)
Ant species richness$_{\text{total}}$	Full model	4	0.72	19.64	0.0001	
	PCA1	1		−7.75	0.0001	−3.19 (0.41)
	PCA2	1		−3.36	0.0021	−1.84 (0.54)
	PCA3	1		−1.68	0.10	
	PCA4	1		2.10	0.04	1.67 (0.79)
Cold climate$_{\text{(individuals)}}$	Full model	4	0.22	2.16	0.09	
	PCA1	1		−2.22	0.03	−1.98 (0.89)
	PCA2	1		1.79	0.08	
	PCA3	1		−0.55	0.58	
	PCA4	1		0.49	0.62	
Cryptic species$_{\text{(individuals)}}$	Full model	4	0.42	5.83	0.0001	
	PCA1	1		−3.88	0.0005	−7.95 (2.05)
	PCA2	1		−1.56	0.12	
	PCA3	1		−1.28	−2.11	
	PCA4	1		2.06	0.05	8.19 (3.97)
Dominant Dolichoderinae$_{\text{(individuals)}}$	Full model	4	0.52	8.61	0.0001	
	PCA1	1		4.79	0.0001	15.67 (6.75)
	PCA2	1		−2.91	0.0067	−12.64 (4.35)
	PCA3	1		1.20	0.24	
	PCA4	1		1.27	0.21	
Generalized Myrmicinae$_{\text{(individuals)}}$	Full model	4	0.10	0.86	0.50	
	PCA1	1		1.36	0.14	
	PCA2	1		−0.66	0.511	
	PCA3	1		−0.82	0.41	
	PCA4	1		−0.69	0.49	
Opportunists$_{\text{(individuals)}}$	Full model	4	0.41	5.44	0.002	
	PCA1	1		−3.58	0.0011	−18.47 (10.64)
	PCA2	1		−2.06	0.048	−14.15 (5.16)
	PCA3	1		−1.69	0.10	
	PCA4	1		−1.34	0.18	
Subordinate Camponotini$_{\text{(individuals)}}$	Full model	4	0.41	5.28	0.0023	
	PCA1	1		−3.70	0.0008	−10.48 (2.83)
	PCA2	1		−0.84	0.41	
	PCA3	1		−2.59	0.01	−13.11 (5.06)
	PCA4	1		−0.11	0.91	

Parameter estimates shown only for significant effects.

abundant in the prairie remnants and two forest types and were significantly lower in the pastures ($F_{3,31} = 17.31$; $P \le 0.0001$).

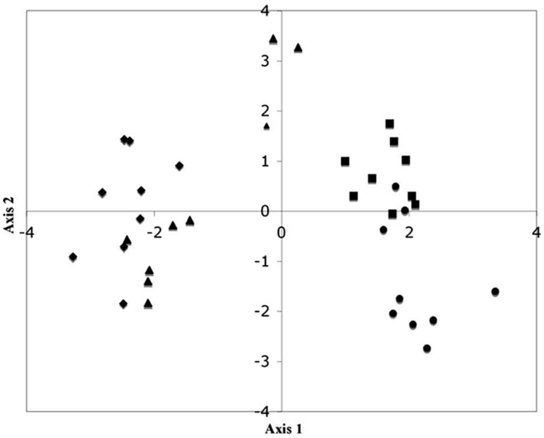

Fig. 5. Plot of the first two PCA axes. Pasture (■), prairie (●), oak-hickory (▲), and flatwoods (◆). PCA axis 1 explained 36.4% of the variation in environmental variables among sites and PCA axis 2 explained 20.7% of the total variation.

Discussion

We determined that ant community structure in the heterogeneous landscape of northeastern Mississippi was hierarchically determined first by edaphic variables, which largely defined floristic associations, and then by the successive factors that define specific microhabitats. Thus, our results are consistent with the study of Andersen (2000) of Australian Formicidae and the recent analysis of Dauber et al. (2006) of the Swedish fauna: ant community structure is determined first by the regional biogeography and patterns of land use rather than localized species interactions or specific floristic composition. Sites with acidic soils and little free Ca^{2+} were forests, and these sites contained the largest number of ant species. Forest ant communities were highly convergent, being composed of species belonging to the cold climate, cryptic, and subordinate Camponotini functional groups. Forest-dwelling ant communities may seem so similar between different forest types because species tend not to differentiate by tree community composition, but are much more responsive to levels of coarse woody debris, litter depth, and soil texture (Yanoviak and Kaspari 2000, Lubertazzi and Tschinkel 2003).

Ants are much more sensitive to incremental changes in herbaceous flora (c.f. Hoffmann 2003), and we suggest that local environmental variation is most important in determining community composition in grassland habitats of northern Mississippi. A number of recent studies corroborate and further emphasize the conclusion that changes in local disturbance regimens influence the seral stage of a given habitat and, thus, alter the composition and structure of herbaceous vegetation. Diversity in the ground-foraging assemblage of ants in semidesert grassland systems is generally negatively correlated with increasing herbaceous cover in ungrazed systems (Hoffmann 2003). Furthermore, encroachment of trees into grassland systems because of disturbance suppression, even single trees, can cause a cascade of changes in ant community structure (Reyes-López et al. 2003, Dauber et al. 2006). In particular, the dominant Dolichoderinae seems to be a group that predominates in areas that experience low levels of stress and disturbance (Andersen 1997, 2000, Boulton et al. 2005). If grazing in these systems affects soil temperature, nest site availability, and food supply similarly to other regions (Forbes et al. 2005), all three of the variables that load positively on PCA axis 2 (which separates pastures from prairies) are correlated with significant grazing and loss of dominant Dolichoderines (Hoffmann and Andersen 2003). Furthermore, the presence of high soil organic matter and low percent sand content found in the pastures can be linked to the influence of grazing. Grazing is known to increase soil organic matter levels through addition of manure and higher rates of fine root turnover, which would proportionally lower the fraction levels of the sand in the soil (USDA 2001, Neff et al. 2005). This may have a negative effect on ants as sandy soils typically provide better nesting sites (Greenslade 1979, Andersen and Spain 1996, Andersen 2000). Finally, the higher number of C_3 graminoids can be attributed mostly to the practice of planting cool season grasses such as *Poa* spp. and *Festuca* spp. in pastures for forage purposes and lower herbaceous height caused by cattle grazing in this region (Ball et al. 1996). These factors reduce the habitat's structural complexity and thus limit nest site and resource diversity and availability, as well as microhabitat capture (c.f. Andersen et al. 2006).

Whitcomb et al. (1972) and Porter and Savignano (1990) suggested that the presence or absence of imported fire ants may be the single most important biotic factor affecting native ant populations. Indeed several studies have shown that fire ants, at least the polygyne form, do have a major impact on native ant communities (Porter et al. 1988, Hooke and Porter 1990, Porter and Savignano 1990, Morris and Steigman 1991). Nevertheless, resilient native ant communities have a good chance of recovering over time as the community is released from fire ant competition as shown by Morrison (2002). Our analysis indicated that other environmental factors, such as the response of grassland flora to grazing or the effect of soil pH on development of the regional flora, may have a more direct effect on the habitat template favored by ants than the presence of *Solenopsis* spp. This further corroborates other experimental studies that suggest that persistent disturbance can prevent recolonization of native ant species rather than the presence of fire ants per se (Lubertazzi and Tschinkel 2003, King and Tschinkel 2006, Tschinkel 2006). In fact, sensitivity to habitat change is why ants have been used bioindicators of habitat change since the early 1980s (see Introduction for references). In this study, native ant numbers were significantly higher in undisturbed and more structurally complex Black Belt prairie habitats (as indicated by PCA axis 2), suggesting that retention of native grasslands may provide a significant source for recolonization of *Solenopsis*-free habitats. Ultimately, however, *Solenopsis* population dynamics suggest that even if nests are successfully removed from a site, continued disturbance from grazing or other human-dominated land use will facilitate their quick reestablishment (e.g., imported fire ants may represent >88% of the ant biomass in actively grazed pastures in Mississippi). Importantly, reducing density of *Solenopsis* but not frequency or intensity of disturbance regimens in managed landscapes may not enhance native ant species.

In the future, land managers trying either to restore Black Belt prairies or to reduce imported fire ant populations in pasturelands should implement strategies such as increased herbaceous diversity and height (but see Lubertazzi and Tschinkel 2003), less C_3 graminoid dominance, and lower cattle stocking levels to promote native ant species abundance and diversity. Clearly, the restoration of native ant faunas in disturbed habitats must consider regional effects of land use history, integrity of the species pool, and species' dispersal ability; simply revegetating a site with native plants is unlikely to be sufficient for faunal reassembly (Dauber et al. 2006, King and Tschinkel 2006). For forest managers, salvage logging and use of prescribed fire that reduce dead woody debris on the forest floor should be discouraged, because this material provides essential nesting sites for many different species of ants (Herbers 1989, Hansen and Klotz 2005). Timber harvest is likely to negatively affect ant species not through the direct removal of tree biomass but by correlated changes in local microclimate and the probability that *Solenopsis* spp. would establish nests along skid roads and other disturbed soils (Tschinkel 2006). Interestingly, ant species seem somewhat tolerant of habitat loss (Golden and Crist 2000, Dauber et al. 2006), although species composition may change if local habitat structure degrades (Sobhrinho et al. 2003). Assuming remnant Black Belt prairies and forested fragments support reasonably intact ant communities, the single best strategy for maintaining the ant communities of this region would be to buffer existing habitats with restored vegetation (Summerville et al. 2006).

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