

Association Between Ants (Hymenoptera: Formicidae) and Habitat Characteristics in Oak-Dominated Mixed Forests

CHANGLU WANG,¹ JOHN S. STRAZANAC, AND LINDA BUTLER

Division of Plant and Soil Sciences, West Virginia University, Morgantown, WV 26506-6108

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ABSTRACT The relationship between ants and their habitats was examined in oak-dominated mixed forests in the central Appalachian mountains. Ants were sampled using pitfall traps over the summers of 1995, 1996, and 1997. Principal component and correlation analysis indicated that ant diversity (Shannon's H'), species richness, and abundance were closely correlated with habitat principal components. Fewer ants, lower number of species, and lower ant diversity were found at sites with higher elevation and soil moisture. Diversity (H') of ants and species richness decreased by 0.1 ($R^2 = 0.75$) and 2.2 ($R^2 = 0.57$) when the elevation increased 100 m, respectively. As the elevation increased, there were relatively less *Formica neogagates* Emery and more *Aphaenogaster rudis* (Emery). More ant species and individuals were found on ridges than in valleys.

KEY WORDS Formicidae, ants, habitat, forest

ANT COMMUNITIES ARE influenced by both abiotic and biotic factors (Cushman 1993, Perfecto and Vandermeer 1996). Distribution of ant species varies along latitudinal gradients, which corresponds to gradual changes in certain environmental factors such as climate and vegetation structure (Greenslade and Greenslade 1977, Majer and Delabie 1994, Touyama and Yamamoto 1997). Ant species and colonies are also influenced by successional stages of forest development. Late successional stages may support long-lived polycalic (multiple nests occupied by a single colony) wood-ant systems, which often cover several hectares or even tens of square kilometers and produce locally high mound densities (Savolainen and Vepsäläinen 1988). Numerous studies demonstrated that habitat modification such as farming, clear-cutting, mining, and fire had strong impacts on ant community diversity and organization. Reduction in the vegetative structure by disturbance may either reduce ant diversity (Room 1975, Greenslade and Greenslade 1977, Majer 1985, MacKay et al. 1991, Lobry de Bruyn 1993, Touyama et al. 1997), increase ant diversity (Wisdom and Whitford 1981, Torres 1984, Puntila et al. 1991), or have no significant effect on ants (Belshaw and Bolton 1993).

Despite the fact that ants are increasingly appreciated as bioindicators for environmental monitoring systems (Andersen 1997, Peck et al. 1998), there remains considerable uncertainty about how different environmental conditions affect ant distributions. In this paper, we document the relationship between ant communities and habitat characteristics in oak-dominated mixed forests. Comparisons were also made

between microhabitats (valleys and ridges). These results may help predict potential impacts of habitat change on ants and the usefulness of using ants to indicate habitat variations and changes.

Materials and Methods

The study was conducted at the George Washington National Forest (GWNF) in Augusta County, VA, and the Monongahela National Forest (MNF) in Pocahontas County, WV. Eighteen 200-ha plots were established. Plots 1 through 9 were located in the GWNF, and plots 10 through 18 were located in the MNF. The distance between the two locations was ≈ 80 km. The distances between adjacent plots in the same location were 1-8 km. This research was conducted in the context of a study on impact of gypsy moth microbial sprays and defoliation on nontarget organisms. Selection of plots were based on good gypsy moth habitat, i.e., oak-dominated forest stands.

Major tree species groups by proportion of total basal area were as follows: oaks (*Quercus* spp.), 54.5%; pines (*Pinus* spp.), 17.2%; maples (*Acer* spp.), 8.6%; and hickories (*Carya* spp.), 7.6%. Typical understory woody plants included mountain laurel (*Kalmia latifolia* L.), witch hazel (*Hamamelis virginiana* L.), pines, dogwoods (*Cornus* spp.), black gum (*Nyssa sylvatica* Marshall), oaks, red maple (*Acer rubrum* L.), striped maple (*A. pennsylvanicum* L.), blueberry (*Vaccinium* spp.), and serviceberry (*Amelanchier arborea* Michaux). More information on the study sites can be found in Wang et al. (2000).

Vegetation of the study plots was investigated in summer of 1996 to determine characteristics of the plots. Within each plot, four parallel 600-m lines, 100 m apart were established to evaluate vegetation charac-

¹ Current address: Stoneville Research Quarantine Facility, USDA-ARS, Stoneville, MS 38776 (e-mail: cwang@ars.usda.gov).

teristics. Seven sampling points per line, or 28 points per plot were marked. Points were located at 100-m intervals along each line at distances between 0 and 50 m from and perpendicular to the line and alternated as to the direction from the line. At each vegetation point, starting at due N and going clockwise, a "Jim-Gem Cruz-All" (an aluminum die-cut gauge for measuring basal area of a forest stand) was used to locate all large trees (≥ 10 cm diameter at breast height [dbh]) in the 10 and 20 BAF (Basal Area Factor) cutouts. The number of included trees and the species of each selected tree were recorded. These numbers gave the basal area of each tree species (multiply by the basal area factor).

Percent canopy cover, herbaceous plant cover, and shrub cover were measured using the following methods: Starting at the vegetation sampling point, three steps were taken in each of the cardinal directions. At that point, a sighting tube was placed over the closed sighting eye and pointed straight upward. Keeping the tube motionless, the observation eye was opened. If the crosshair hit vegetation, it was scored as "positive." Otherwise it was scored as "negative." The sighting tube was then pointed downward and the process repeated. A "positive" score can be herbaceous plant cover (< 0.5 m in height) or shrub cover (≥ 0.5 m in height). The process was repeated to obtain five samples in each of the four cardinal directions. Density of small trees was measured in a 7 by 7-m area centered at each of the vegetation sampling points. All trees with dbh of < 10 cm were tallied by species.

Five soil samples were taken from each of the 18 plots on the same day (30 July 1996) to ensure they were influenced by similar previous weather conditions. Two samples were taken from the center of the two pitfall sites, and the other three samples were taken on an 80 m long transect between the two pitfall sites. Soil samples were taken from the mineral soil layer ("A" layer). The samples were brought to the laboratory and the wet weight measured. The samples were then dried at 90°C for 48 h, and water content derived by the difference between dry and wet weight over wet weight. All study plots had similar soil types except plot 10 (in MNF) had more rocks.

Ants were sampled using pitfall traps. In each plot, a higher site (ridge) and a lower site (valley) were selected. They were all within the vegetation sampling area. The elevation differences between the two sites at each plot were 39 ± 28 m (mean \pm SE). The lower sites (valleys) were generally more moist than the upper sites (ridges) due to the proximity to a stream or patterns of surface water runoff and less exposure time to sunlight. The arrangement of the pitfall trap sites in plots 5, 8, 9, and 10 were exceptions to this rule due to difficulties in finding appropriate sampling sites. The two pitfall trap sites in these plots were all on ridges. At each site, a set of nine traps was arranged in a grid of 3 by 3 m in 1995. The design was changed to six traps arranged in a 15 m diameter circle in 1996 and 1997. This change was intended to collect more diverse ants through a larger sampling area than that in 1995. The traps were emptied weekly from mid-May

to mid-August from 1995 to 1997. Each trap contained an outer liner, a funnel, and an inner storage cup. The outer liner was a 454-ml plastic cup with a top diameter of 92 mm and depth of 105 mm. The inner cup was a 100-ml capacity plastic cup with a top diameter of 58 mm and depth of 55 mm. The funnel rests on the edge of the outer liner and extends into the storage cup. The storage cup was filled with propylene glycol as preservative and killing agent. For each trap, the whole set of cups was hung from the center hole of a wood board ring with 21.5 cm diameter. The wood ring was placed flush with the ground, and its surface was covered with a thin layer of sand, which made its color and texture similar to that of the ground. The wood ring greatly reduced the amount of soil falling into the pitfall trap and made the sorting of the specimens much easier. The traps were covered by a clear plastic cover as a rain shield which was supported by metal wires. Because too much disturbance occurred in 1995 and 1996, a large fence (1.5 m diameter, 80 cm high) was established around each pitfall trap in 1997 to deter large animals.

All ants were identified to species using Creighton (1950), Lynch (1987), and Wilson (1955). Species richness, abundance, and diversity (Shannon's H') (Shannon and Weaver 1949) of each plot were summarized or calculated. Voucher specimens from the study were deposited in the Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, CA, and in the West Virginia University Arthropod Collection.

Because the number of habitat variables is large and many of them were correlated with each other, principal component analysis was performed on vegetation, soil moisture, and elevation characteristics of the study plots (total of 32 variables). This transformation served to extract the underlying factors that distinguish the plots and to reduce the 32 variables to a few important principal components (Davis 1986). Each principal component is a linear combination of the original variables. The loading (or weight) of each variable determines its contribution to that principal component. The correlation between the first two habitat principal components and ant abundance (log transformed), species richness, and diversity index (H') were calculated. Plots 10 and 12 were not included because very low numbers of ants were collected due to disturbance. The correlations between the relative abundance of the first five most abundant ant species with the first two habitat principal components were also calculated. The relative abundance of the ant species was square root transformed before analysis. Regression analysis was performed between ant species richness and elevation of the plots as model $y = b_0 + b \times \text{elevation}$. Two-way analysis of variance (ANOVA) was used to compare ant species richness between microhabitats (valley versus ridge) and forests. Ants from three plots of the GWNF (plots 5, 8, and 9) and two plots from MNF (plots 10 and 12) were excluded from this analysis. As mentioned before, plots 5, 8, 9, and 10 had the two pitfall sites all on similar microhabitats. Plot 12 was excluded because only 43

Table 1. Physical and vegetative characteristics of the plots in the George Washington (GWNF) (plots 1–9) and Monongahela (MNF) (plots 10–18) National Forests

Variable	Plot																		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	
Elevation (m)	628	564	518	663	722	599	610	697	718	1,138	1,077	1,219	871	871	935	863	792	752	
Soil moisture content (%)	13.6	11.4	10.7	10.6	11.1	8.9	11.4	10.0	7.1	31.4	25.8	27.4	19.5	19.0	22.0	18.4	19.5	18.7	
Coverage																			
Canopy	80.7	87.3	86.7	81.2	83.7	80.8	79.0	82.8	77.8	88.0	90.7	91.3	93.5	89.9	84.6	89.1	85.2	93.4	
Herbaceous plants	50.9	31.9	24.1	43.4	31.1	39.2	32.6	32.6	34.7	22.5	17.1	47.1	31.1	38.8	26.1	25.0	23.7	37.1	
Shrub	19.4	18.0	26.5	21.5	29.0	31.5	22.7	18.6	43.8	16.7	17.0	22.5	40.9	25.3	43.1	27.1	17.1	18.8	

ants were captured during 3 yr of sampling, and therefore species richness data from this plot is not reliable. Ant abundance from 1997 sample was also compared between microhabitats and forests by two-way ANOVA. Plots 5, 8, 9, and 10 are excluded from this analysis. The ant abundance from 1995 and 1996 samples was not analyzed because of high percentages of disturbance by large animals. Ant abundance data were log transformed to normalize the data before ANOVA analysis. All statistical analysis was done using SAS software (SAS Institute 1999).

Six percent of the traps were disturbed partially or completely in 1997 samples. The number of ants in a pooled sample was adjusted according to the number of traps disturbed and the degree of disturbance. If a trap was completely disturbed, the ant count was adjusted by 6/5, because a sample consisted of six traps in 1997. If a trap was partially disturbed, the count was adjusted by 6/5.5. On one occasion, the whole set of traps in one site was totally disturbed, and the sample was estimated by the average number of ants from the other 14 wk at the same site.

Results

Physical and Vegetation Characteristics of the Plots.

The soil moisture calculated from soil samples taken on 30 July 1996, the elevation, and the vegetation characteristics of the study plots are shown in Table 1. Total large tree counts of the following 10 most common species on the 28 grid points of each study plot were recorded: oaks, pines, maples, hickories, ashes (*Fraxinus* spp.), black gum, black locust (*Robinia pseudoacacia* L.), dogwoods, eastern hemlock [*Tsuga canadensis* (L.) Carriere], and sweet (black) birch (*Betula lenta* L.). The small tree counts of the following 17 understory species (genera) at the 28 grid points of each study plot were recorded: serviceberry, hickory, American chestnut [*Castanea dentata* (Marshall) Borkhausen], dogwood, ash, witch hazel, mountain laurel, black gum, ironwood [*Ostrya virginiana* (Miller) Koch], pines, oaks, azalea (*Rhododendron*

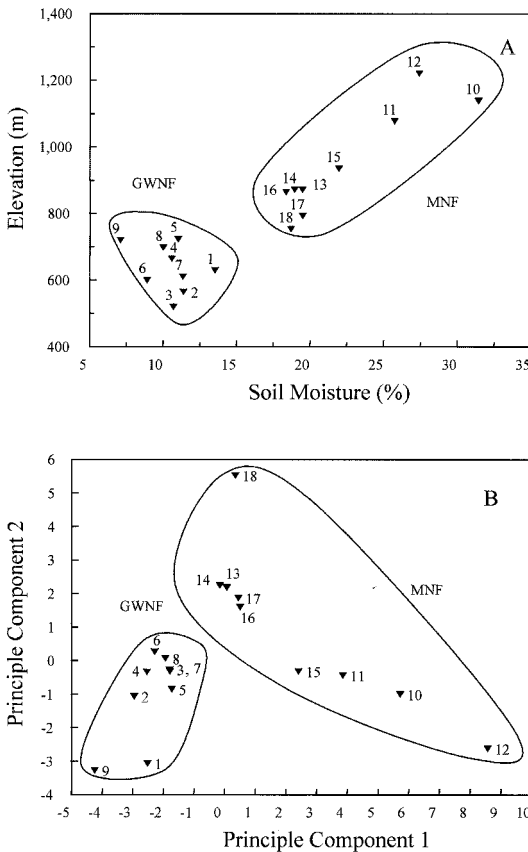


Fig. 1. Ordination of the plots by the two most important habitat variables (A), and by the first two habitat principal components (B).

Table 2. Relative abundance of the 10 most common ant species collected from pitfall traps during 1995 to 1997 in the George Washington (GWNF) and the Monongahela (MNF) National Forests

Ant species	Percentage (%)	Abundance
<i>Camponotus pennsylvanicus</i> (De Geer)	23.3	7,405
<i>Aphaenogaster rudis</i> (Emery)	13.6	4,327
<i>Formica neogagates</i> Emery	11.5	3,638
<i>Myrmica punctiventris</i> Roger	10.3	3,271
<i>Myrmica</i> n.sp. 1	8.4	2,669
<i>Lasius umbratus</i> (Nylander)	4.5	1,415
<i>Tapinoma sessile</i> (Say)	4.2	1,330
<i>Prenolepis imparis</i> (Say)	4.2	1,321
<i>Lasius alienus</i> (Foerster)	4.1	1,299
<i>Formica subsericea</i> Say	3.3	1,039
Total	87.4	27,714

Table 3. Correlation coefficients between ant community variables and the first two habitat principal components

Principal component	n	Diversity (H')	Abundance ^a	Species richness
1	16	-0.75**	-0.81**	-0.77**
2	16	-0.40	-0.51*	-0.53*

*, significant (≠0) at α = 0.05; **, significant (≠0) at α = 0.01.

^a Only 1997 data is included because of excessive disturbance in the other two years.

spp.), black locust, sassafras [*Sassafras albidum* (Nuttall) Nees von Esenbeck], eastern hemlock, blueberry, and maples.

The large and small tree counts, plus the five variables listed in Table 1 were used to represent the characteristics of each plot. Many of these variables are correlated with each other. For example, the number of large maples is positively correlated with soil moisture (n = 18, r = 0.87, P < 0.01) and elevation (n = 18, r = 0.81, P < 0.01); the soil moisture is positively correlated with elevation (n = 18, r = 0.91, P < 0.01). Principal component analysis showed that the first principal component represented 34% of the total variance of all components. The first five principal components comprised 76% of the variance.

The first five variables that contributed most to the first principal component were elevation (loading 0.28), soil moisture (loading 0.28), basal area of large hickories (loading 0.26), maples (loading 0.25), and ash (loading 0.25). All of these five variables were positively correlated with each other (n = 18, r ≥ 0.62, P ≤ 0.01). The first principal component probably measures the overall trend in soil moisture and elevation of the plots. This is partly shown by the remarkable similarity between Fig. 1A and B. The second principal component, which represented 14% of the total variance of all components, was mainly explained by the basal area of large hemlocks (loading 0.34) and number of small pines (loading 0.33). Ordination of the plots by the two most important habitat variables (elevation and soil moisture) and by the first two habitat principal components showed a clear separation of the GWNF plots from the MNF plots (Fig. 1), which coincided with the geographical separation of the plots. Plots with higher soil moisture and elevation were located farther to the right on the horizontal axis.

Ant Communities and Their Relationships with Habitat Characteristics. A total of 31 species of ants was collected from the 18 plots during 3 yr of sampling. The numbers of ants collected during 1995–1997 were

12,972, 11,830, and 6,930 respectively. The 10 most abundant ant species comprised 87.4% of the samples (Table 2). There were strong negative correlations between the first principal component, ant diversity, abundance, and species richness (Table 3). Thus, ant abundance, diversity, and species richness were negatively correlated to elevation and soil moisture. Ant abundance and species richness were also negatively correlated with the second principal component.

Correlation analysis of the relative abundance (square root transformed) of each of the five most common ant species from 1995 to 1997 pitfall samples with the first two habitat principal components showed *Formica neogagates* Emery and *Aphaenogaster rudis* (Emery) were all closely correlated with the first habitat principal component (Table 4). Therefore, as the elevation increased, there were relatively fewer *F. neogagates* and more *A. rudis*.

Because elevation is a relatively stable and easy variable to measure, we performed regression analysis between ant diversity, species richness, and elevation of the plots based on pitfall samples (Table 5). According to the regression equation, ant diversity (H') decreased by 0.1 when the elevation increased 100 m (F = 40.9, df = 1, 14; P < 0.01). Species richness decreased by 2.2 when the elevation increased 100 m (F = 18.8; df = 1, 14; P < 0.01). There was also an association between ant abundance in 1997 samples and elevation of the plots (F = 23.9; df = 1, 15; P < 0.01). If soil moisture and elevation were both added to the equations, the regression slopes for both elevation and soil moisture would be insignificant (P > 0.05) because of their strong correlation.

Effect of Microhabitats on Ants. The ant abundance (log transformed) and species richness between valleys and ridges were compared (Table 6). Valleys had significantly fewer individuals (F = 4.4; df = 1, 24; P = 0.048) and fewer species (F = 14.5; df = 1, 22; P < 0.01) than ridges. There was no interaction effect between forests and microhabitats on ant abundance (F = 0.5; df = 1, 24; P = 0.50) and species richness (F = 0.6; df = 1, 22; P = 0.44).

Besides the differences in ant abundance and species richness, there were also differences in species composition between valleys and ridges. In the GWNF, the ridges had one more species, *Monomorium minimum* (Buckley), than valleys. This species usually lives in dry areas (Wheeler et al. 1994). In the MNF, two species were unique in valleys, six species were unique on ridges (Table 7).

Table 4. Correlation coefficients between ant species relative abundance and the first two habitat principal components

Principal component	n	Ant species				
		<i>C. pennsylvanicus</i>	<i>A. rudis</i>	<i>F. neogagates</i>	<i>M. punctiventris</i>	<i>M. n.sp. 1</i>
1	16	0.24	0.66**	-0.64**	0.09	-0.48
2	16	0.17	0.07	-0.57*	0.60*	-0.26

*, significant (≠0) at α = 0.05; **, significant (≠0) at α = 0.01.

Table 5. Regression between ant diversity, species richness, abundance and elevation of the study plots

Regression equation	<i>n</i>	<i>R</i> ²	Estimate of parameter variance
Diversity (<i>H'</i>) = 1.63 - 0.001 × elevation	16	0.75	<i>b</i> ₀ : SE = 0.12; <i>t</i> = 13.9; <i>P</i> < 0.01 <i>b</i> : SE = 0.00015; <i>t</i> = -6.4; <i>P</i> < 0.01
Species richness = 38.4 - 0.022 × elevation	16	0.57	<i>b</i> ₀ : SE = 3.9; <i>t</i> = 9.8; <i>P</i> < 0.01 <i>b</i> : SE = 0.005; <i>t</i> = -4.3; <i>P</i> < 0.01
Abundance (log) ^a = 4.01 - 0.0020 × elevation	17	0.69	<i>b</i> ₀ : SE = 0.27; <i>t</i> = 14.7; <i>P</i> < 0.01 <i>b</i> : SE = 0.0003; <i>t</i> = -5.8; <i>P</i> < 0.01

^a Data is based on 1997 samples only.

Discussion

This study showed strong relationships between ant communities and the physical characteristics of the plots. Fewer ant individuals, lower diversity, and less number of species occurred at sites with higher elevation and soil moisture. The results agree with those studies in Japan (Touyama and Yamamoto 1997), Madagascar (Fisher 1996), and in Panama (Olson 1991) which also showed a negative relationship between ant species richness and elevation (*r* = -0.85, -0.97, and -0.96, respectively). The decrease of ant species richness, diversity, and ant abundance in response to elevation increase might be the result of lower temperatures at higher elevations. MNF plots are at higher elevations than GWNF plots and have lower temperatures. Low winter temperature in mountain temperate forests could be the limiting factor for the survival of some ant species and colonies. Lower annual median temperature might cause lower ant activities, and therefore, lower catches in pitfall samples. The average minimum temperature in January was -9.2°C and -6.7°C recorded from three nearby weather stations around the MNF plots and five weather stations near the GWNF plots, respectively (Wang et al. 2000). Annual median temperature around the MNF plots was 1.6°C lower than that of GWNF plots. Fewer species and fewer ants were recorded from MNF plots (Table 6).

The study plots showed distinct differences in soil moisture content, which is positively correlated with the elevation of the plots. As a result, a close negative correlation was also found between soil moisture and ant species richness and abundance. The differences in ants between valleys and ridges seem to support this association, because the valley sites of the plots are close to intermittent streams and therefore are typically more moist than ridges. However, the differences

in microclimate such as temperature between ridges and valleys might also be related with the ants. The association of soil moisture with ants might be a coincidence of correlation between soil moisture and elevation. Levings (1983) suggested that soil moisture influences ants through foraging activity, food abundance, suitability of nest sites, and predation by other ants. Considering there were very diverse trees, shrubs, and abundant wood materials in the plots, we speculate that ants would not be influenced by moisture through the changes in food or suitability of nesting sites. Because long distances between plots require much time and several people, we collected same-day soil samples only once. An average of multiple samples would be more accurate to determine the degree of association between soil moisture and ants. Other soil variables that might have associations with ant distributions and abundance, viz., water retention difference (WRD), pH, % sand, % clay, % organic matter, and organic layer depth at pitfall sampling sites were measured in 1998. Only WRD was detected with close relationships with ant variables (unpublished data). However, WRD is positively correlated with soil moisture and has smaller *R*² with ant variables than soil moisture does. Therefore, only one soil variable is included in this paper.

Besides elevation and soil moisture, the basal areas of hickories, maples, and ash are also important variables that contribute to the first principal component. So, there was also an association between ant communities and vegetation characteristics based on the principal component analysis. These three tree species accounted for 17% of the trees based on basal area. However, there were no obvious close relationships between these vegetation variables and certain ant species. This association might be merely a reflection of their correlation with soil moisture and elevation.

Table 6. Comparison of ant abundance (from 1997 samples) and species richness (from 1995–1997 samples) between microhabitats and forests

Microhabitat	Forest ^a							
	GWNF				MNF			
	<i>n</i>	Abundance	<i>n</i>	Species richness	<i>n</i>	Abundance	<i>n</i>	Species richness
Valley	6	166 ± 15Aa	6	21.0 ± 1.0Aa	8	47 ± 13Ba	7	11.3 ± 0.7Ba
Ridge	6	422 ± 63Ab	6	24.0 ± 1.0Ab	8	74 ± 16Bb	7	15.9 ± 1.2Bb

Means ± SE; means within a row or column followed by different letters are significantly different (*P* < 0.05, two-way ANOVA). Upper case letters indicate comparisons between columns (forests); lower case letters indicate comparisons between rows (microhabitats).

^a GWNF = George Washington National Forest, and MNF = Monongahela National Forest.

Table 7. Number of unique species, and individuals collected from different microhabitats in the Monongahela National Forest plots from pitfall trap samples (1995–1997)

Valley		Ridge	
Ant species	Number	Ant species	Number
<i>Tetramorium caespitum</i> (L.)	2	<i>Camponotus americanus</i> Mayr	2
<i>Crematogaster lineolata</i> (Say)	8	<i>Camponotus subbarbatus</i> Emery	4
		<i>Prenolepis imparis</i> (Say)	2
		<i>Dolichoderus plagiatus</i> (Mayr)	8
		<i>Myrmica pinetorum</i> Wheeler	1
		<i>Leptothorax schaumii</i> Roger	1

Caution should be taken in interpreting the results of this study, because there were only 18 plots. More study plots will increase the accuracy of estimation results. The sampling scheme in this study was part of a design for other study objectives. For environmental monitoring purposes, it is not necessary to take samples as long as we did in this experiment. However, the sampling period should be long enough to document most of the ant species.

Many environmental variables can be associated with ants, and they may correlate with each other. It is important to identify the inherent factors, and study their relationship with the ant communities. When the inherent environmental factor is not clear, principal component analysis or discriminant analysis of the habitat variables can be performed. Although they do not give relative importance of the variables that are correlated with each other, they do provide information on the most important factors. In our study, we used principal components of the habitat variables to study their relationship with ant communities. This helped reveal the inherent most important habitat factor and simplified the calculation process.

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