EFFECTS OF HISTORICAL LAND USE AND FOREST PATCH SIZE ON MYRMECOCHORES AND ANT COMMUNITIES

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Abstract. We studied the effects of patch size and historical land use on woodland ants and myrmecochores (plant species that have their diaspores dispersed by ants) in mesic forests of the southern Appalachian Highlands. Our purpose was to examine a potential mechanism, the presence and diversity of seed-dispersing ants, that might explain the reduced abundance and diversity of myrmecochores in small forest patches with high intensities of past land use. Small patches (<25 ha) of forest harbored a greater abundance and diversity of myrmecochorous ants, but a lower abundance and species richness of myrmecochores than large patches (>200 ha) with minimal past land use. Overall, sites with greater myrmecochore species richness and abundance had less diverse ant communities and a lower abundance of ants. However, ant species composition varied with patch size. Large patches with low historical land-use intensity were dominated by one ant species, *Aphaenogaster fulva*, whereas small patches supported higher numbers of *Aphaenogaster rudis* and two *Camponotus* species. The abundances of immature myrmecochores were more strongly related to land-use history, forest patch size, and the abundance of mature conspecifics than to ant variables. An absence of seed-dispersing ants cannot explain the reduced numbers of myrmecochores in small patches with high past land use because seed dispersal by ants still appears to be available in those patches. Land-use legacies or fragmentation effects may be overriding any advantages offered by the increased diversity and abundance of ants at those sites.

Key words: ants; Appalachian Mountains; Blue Ridge Mountains; forest patch size; fragmentation; herbaceous vegetation; land use; myrmecochory; North Carolina.

INTRODUCTION

Understanding the complex ecological effects of land-use patterns and history remains a formidable but important challenge for ecologists (Turner et al. 1998, Dale et al. 2000). The consequences of habitat fragmentation have been extensively studied, and the ecological legacies of prior land use are now recognized as important (e.g., Duffy and Meier 1992, Foster 1992, Foster et al. 1992, Pearson et al. 1998). A persistent effect of prior land use has been observed in plant community composition in temperate (Foster 1992, Motzkin et al. 1996, Pearson et al. 1998) and tropical (Foster et al. 1999) forests; stream invertebrate assemblages (Harding et al. 1998); abundance of riparian coarse woody debris (Christensen et al. 1997); and land-cover patterns (Spies et al. 1994, Wallin et al. 1994). Given the extensive cover of secondary forest across much of the eastern USA, distinguishing between the effects of past land use and current patch characteristics on the structure and function of ecosystems is important (Primack 1992, Solbrig 1992). We examined the effects of forest patch size and past land use on myrmecochores (ant-dispersed herbaceous

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plants) and ants in the mesic forests of the southern Appalachian Highlands, USA.

The southern Appalachian Mountains are dominated by extensive secondary forests characterized by a species-rich understory herbaceous community (Braun 1950). Many areas were subjected to forest clearing and planted in row crops or intensively grazed. The poor suitability of much of the region for agriculture and increasing opportunities for nonfarm income led to widespread land abandonment. Natural reforestation produced extensive forests and increased the frequency of large successional patches across the landscape (Phillips and Shure 1990), but past land use had lasting effects in southern Appalachian forest communities (e.g., Wales 1972, Phillips and Shure 1990, Matlack 1994, Meier et al. 1995, Pearson et al. 1998). The current presence and abundance of native mesic forest herbs in the southern Appalachians is correlated with forest patch size and past land use. Species richness and abundance are greater in large (>200 ha) than small patches (<25 ha), and several native mesic forest herbs are less abundant or absent in forest patches that experienced intensive past land use (Pearson et al. 1998). Abundance of liliaceous species (e.g., *Disporum lanuginosum*) is substantially reduced in forest patches characterized by prior agricultural uses, even in large patches. Species with very limited dispersal (e.g., *Viola*

spp.) are absent or scarce in small forest patches, although wind-dispersed species (e.g., some ferns and composites [Asteraceae]) are not affected by patch size. Myrmecochorous species (e.g., *Disporum maculatum* and *Uvularia grandiflora*; Table 1) are more likely to be absent in small patches, suggesting a linkage to the presence and abundance of seed-dispersing ants. Although the landscape is dominated by forest, the size and configuration of forest patches vary, with small patches also being relatively isolated. If seed-dispersing ants were absent in small patches, this would suggest that dispersal limitations may explain, in part, the distribution of myrmecochorous species.

Myrmecochory (seed dispersal by ants) is an important plant–animal mutualism with direct relevance to plant reestablishment following disturbance (Andersen and Morrison 1998). Ants are responsive to changes occurring at small spatial and temporal scales (Talbot 1934, Puntilla et al. 1991, Kremen et al. 1993, Crist and Wiens 1994), and habitat disturbance can disrupt ant-facilitated seed dispersal, with profound consequences for plant population dynamics (Andersen and Morrison 1998). Ant-dispersed species (myrmecochores) may comprise 35–40% of herbaceous species and up to 75% of all emergent herbaceous stems in eastern U.S. forests (Beattie and Culver 1981). Myrmecochorous guilds are generally tolerant of heavy shading (Beattie and Culver 1981), whereas non-ant-dispersed species are more prevalent in locations with more sunlight, higher soil temperatures, and lower soil moisture. Following seed fall and capsule dehiscence in late spring, myrmecochore diaspores (seeds) are located rapidly by ants (e.g., *Aphaenogaster*, *Camponotus*, *Crematogaster*, and *Formica* spp.) and taken into their nests. The fleshy and lipid-rich food body called the elaiosome (thought to be the main ant attractant) is then removed (Westoby et al. 1991, Hughes and Westoby 1992*a*, Gomez and Espalder 1998). In contrast to seed predation by rodents, the seed is not normally consumed by ants and is discarded in or relocated from the nest (Beattie and Culver 1981, Kjellsson 1985). Mean seed dispersal distance by ants is ~1 m, with nearly all dispersal distances ranging from 0–2 m (Andersen 1988*b*, Hughes and Westoby 1992*a*, Gomez and Espalder 1998).

We examined the effects of patch size and historical land use on a suite of mesic forest myrmecochores and ant populations. We addressed the following questions: (1) Do ant species richness and ant abundance vary among mesic forest patches that differ in size and intensity of prior land use? We hypothesized that ant diversity and abundance would decrease with smaller patch sizes and higher levels of land-use intensity. (2) Are myrmecochores most abundant and diverse in locations where ants are also most abundant and diverse? We hypothesized that adult myrmecochore abundance and species richness would be positively correlated with ant abundance and richness between and within

sites. We also hypothesized that the abundance of immature (seedlings and juveniles) myrmecochores would be positively related to (a) ant abundance and diversity and (b) adult myrmecochore abundance between and within sites. (3) What explains the variability in ants and myrmecochores at broad scales (sites) and at fine scales (sampling points)? We hypothesized that ant abundance and diversity would be positively related to the abundance and species richness of adult myrmecochores at broad and fine scales.

METHODS

Study sites

Study sites were located in the French Broad River Basin on public and private lands in Madison and Buncombe counties of western North Carolina (Fig. 1). Sites were classified according to (1) forest patch size (large or small) and (2) past land-use intensity (high or low). Forest patches <25 ha in area were classified as small; all small patches also had high intensity of past land use (small–high sites, $N = 9$). Forest patches >200 ha in area were classified as large and varied in past land-use intensity (large–high sites, $N = 10$; large–low sites, $N = 5$). The patch size–land use designations (e.g., large–low, large–high, and small–high) will be used subsequently throughout this paper. Sites with high-intensity past land use had a history of cultivation or grazing and were logged in the 1940s or more recently; most small patches were privately owned woodlots. Sites with minimal past land use were located in large patches of older forest that were never cleared for agricultural use and had not been logged in >85 yr or had never been logged. All study sites were in closed-canopy, mesic, deciduous forest at 600–1200 m elevation and were dominated by saw-timber sized (>50 cm diameter at breast height [dbh]) trees. Dominant canopy species included *Liriodendron tulipifera*, *Acer saccharum*, *Acer rubrum*, *Quercus* spp., *Tilia americana*, *Carya* spp., and *Betula lenta*.

Field sampling

Ant diversity and abundance were sampled at each study site ($N = 24$) from 28 June to 29 July 1999, corresponding to the time period of seed production by myrmecochores. Sampling was conducted using a fixed area (40×40 m) in all patches to control for species-area effects (Palmer 1991). Sampling of sites was randomized to compensate for any seasonal differences in ant activity. Each study plot consisted of a grid of 25 bait stations arranged in five lines with sampling points separated by a distance of 10 m. The 10-m separation distance between baits was chosen to treat points as independent samples because seed dispersal by ants rarely exceeds 1–2 m (Hughes and Westoby 1992*a*).

Baits (2–3 mL tuna preserved in oil) were placed at each of the 25 sampling points by 0900 and checked hourly until 1530. This bait was used because tuna oil
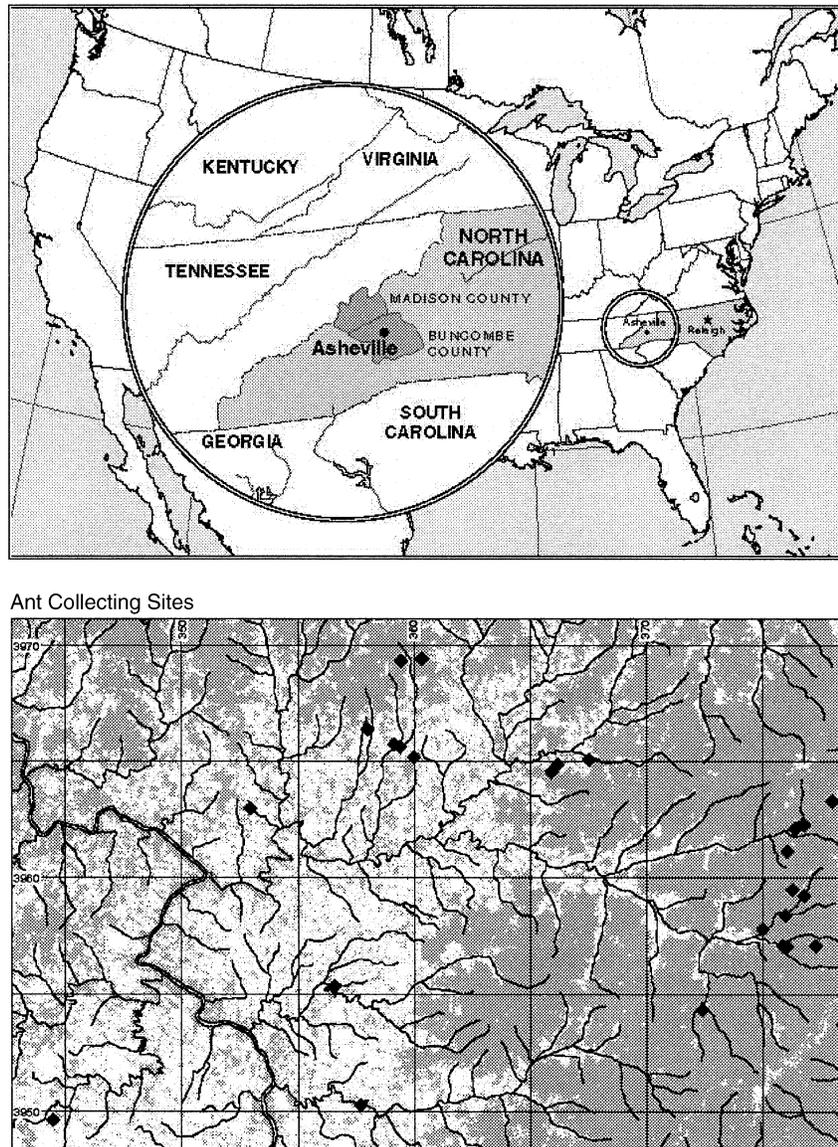
FIG. 1. The upper panel shows the location of the southern Appalachian study region, Madison and Buncombe Counties, North Carolina. The lower panel illustrates the distribution of ant collecting sites (black diamonds) in the study region with a 5-km grid overlain. Deciduous forest is shaded gray, and streams are shown in black.

and the elaiosomes of myrmecochore fruits have a similar diglyceride (Marshall et al. 1979). Ant activity ceased with moderate or light rain; therefore, sampling was conducted only when rain did not penetrate the canopy. Ant collections were made and the time noted when ≥5 workers were present at a bait. Specimens were preserved in 70% EtOH (ethyl alcohol) and later identified to species. Voucher specimens of all species were donated to the Entomological Museum at the University of Wisconsin-Madison.

The diversity and abundance of myrmecochores (Table 1) were censused at each site. Presence–absence of each plant species was recorded within a 2 m radius around each bait station. Age classes of myrmecoc-

hores were recorded as immature (seedlings of the year and larger prereproductive plants) or adults (reproductive) based on size, leaf scars, rhizome presence, and fruit production. In addition, the number of emergent stems for each species was recorded in three 0.5-m^2 quadrats randomly placed within the 2 m radius surrounding each bait.

Understory and canopy cover were recorded at each of the 25 bait stations at each site. Understory cover (1–3 m in height) was classified as none, low, medium, or high based on leaf and woody stem density directly above the 2 m radius area surrounding each bait. These understory categories were calibrated from 1–2 m and 2–3 m by counting the number of times a 2-m pole

TABLE 1. Myrmecochores in the southern Appalachian Highlands that were sampled in this study.

Species	Common name	Family
Anemone quinquefolia	windflower	Ranunculaceae
Asarum canadense	wild ginger	Aristolochiaceae
Carex spp.	sedges	Cucurbitaceae
Disporum lanuginosum	yellow mandarin	Liliaceae
Disporum maculatum	speckled mandarin	Liliaceae
Hepatica acuta	sharp-lobed liver leaf	Ranunculaceae
Hepatica americana	round-lobed liver leaf	Ranunculaceae
Erythronium americanum	trout lily	Liliaceae
Sanguinaria canadensis	blood root	Papeveraceae
Tiarella cordifolia	foam flower	Saxifragaceae
Trillium grandiflorum	large-flowered trillium	Liliaceae
Trillium erectum	wakerobin	Liliaceae
Uvularia grandiflora	large-flowered bellwort	Liliaceae
Uvularia perfoliata	perfoliate bellwort	Liliaceae
Uvularia pudica	mountain bellwort	Liliaceae
Uvularia sessilifolia	sessile bellwort	Liliaceae
Viola blanda	sweet white violet	Violaceae
Viola canadensis	Canada violet	Violaceae
Viola hastata	halberd-leaved violet	Violaceae
Viola pubescens	hairy violet	Violaceae
Viola rotundifolia	round-leaved yellow violet	Violaceae
Viola sororia	common blue violet	Violaceae

Note: List compiled from Handel (1976), Beattie and Culver (1978, 1981), Beattie et al. (1979), Pudlo et al. (1980), and Handel et al. (1981).

placed at 20 predetermined points around the bait intercepted any vegetation (Mitchell 2000, adapted from Mills et al. 1991). Canopy cover was recorded at each bait by using the fixed area of a mirror to view the reflection of the canopy immediately above the point. Canopy cover was assigned a value by class: 0–20, 20–40, 40–60, 60–80, or 80–100%.

A composite soil sample for each site was obtained by combining samples of the top 10 cm of soil (after leaf litter was removed) from four randomly placed points within the plot. Soils were dried at 70°C for 48 h and analyzed at the Soil Testing Laboratory of the North Carolina Department of Agriculture, Agronomic Division, Raleigh for soil chemistry, texture, nutrient availability, and organic matter. Topographic information, including terrain shape, slope, aspect, and elevation, was also recorded for each site.

Data analyses

Ant abundance at the site level was compiled by counting the number of bait stations attended by each species. Ant species richness was computed by counting the number of species collected at individual bait stations and for the entire site. Analysis of variance (ANOVA) was used to determine whether ant species richness and abundance varied among sites that differed in patch size and land use (PROC GLM, SAS 1990). When the ANOVA yielded a P value ≤ 0.05 for main effects, a least significant difference multiple comparison test was used to test for significant differences among treatments.

Species richness and abundance of myrmecochores were also computed for each site. Myrmecochore abundances for each bait station were calculated by summing the counts of myrmecochores made within the three quadrats at each bait. To compile site-level data, myrmecochores were summed for all species across all bait stations for each site. Myrmecochore counts were also summed across selected taxa (i.e., Liliaceae and Violaceae families) to examine effects on taxonomic groupings and to eliminate low counts of certain species. Synthetic grouping is appropriate because most myrmecochorous ants are generalists, inclined to take a wide variety of available seeds as long as it is physically possible for them to disperse the seeds (Beattie et al. 1979). Furthermore, rates of removal and distance dispersal curves generated by myrmecochory are not specific to particular seed species (Hughes and Westoby 1992*b*, Andersen and Morrison 1998).

Relationships between ants and myrmecochores: canonical correlation analysis.—The relationship between ants and myrmecochores was investigated with canonical correlation analysis (Johnson and Wichern 1988). Given the relationship between ants and plants of different ages, we were careful in selecting which myrmecochore age classes were appropriate as dependent and independent variables. When the dependent variable was immature myrmecochores, the independent variables were those measuring the abundance of conspecific adult myrmecochores and ants because adult plants must be present to provide the seed source (question 2, immature plants = treatment + ants + adult). When an ant variable was used as a response (question 3), adult myrmecochores were the only herbaceous independent variables used in the models because adult plants produce seeds used by ants (ants =

treatment + adult plants). An ordinal dummy variable (treatment) was used to indicate patch size/land use category for each site (1 = small–high; 2 = large–high; and 3 = large–low). These analyses were conducted for two different spatial scales: among sites using site-level data and within-sites using bait station-level data. Only canonical correlations with $R > 0.65$ were considered informative. Relationships between independent and dependent variables were assessed by examining the canonical redundancy analysis and the correlation coefficients between the original variables and the canonical variates output by PROC CANCORR (SAS 1996). Original variables having $R > 0.30$ were considered to be correlated with their respective canonical variate.

Relationships between ants and myrmecochores: analysis of variance.—To supplement the canonical correlations, ANOVA was used to test for more complex relationships among variables. To determine relationships of myrmecochores (both age classes and taxonomic groups described above), ants, and environmental variables among sites, we utilized a mixed model ANOVA (PROC MIXED, SAS 1990). For within-site analyses, PROC MIXED allowed for independent variables to be nested within the patch size/land use treatment and assigned as random effects while patch size/land use was set as a fixed effect. When bait-level data were binary (e.g., the presence or absence of a particular ant species), a logistic approach was utilized (PROC GENMOD, SAS 1990). Myrmecochore sums were square-root transformed prior to analysis. For each model, a scatter plot of residuals was examined to check the normality and equality of variance of data used in the models. There was no evidence of a heteroscedastic trend in the data. Results that revealed patterns already described by the canonical correlations were not reported.

A repeated-measures statement that accounted for spatial autocorrelation between sampling points was added to within-site models. Although we chose a distance between sampling points that should have reduced such correlation (in terms of ant dispersal distances), we took this added measure to account for autocorrelation in dependent or independent variables. Comparisons of output from models that did and did not account for spatial autocorrelation showed no significant differences in P values.

Difference in habitat characteristics.—Mean values of the habitat measures for the patch size/land use categories were compared using ANOVA and multiple comparisons tests. Factor analysis was used to examine the covariance structure of habitat variables at the scale of the study site. Variables included soil information, elevation, tree canopy, and understory cover, and the ordinal value assigned to patch size/land use categories. Mean values for tree canopy and understory cover were used to represent variation in woody vegetation structure at each site. The analysis employed the PROC

TABLE 2. Total ant abundance (measured as number of baits attended) and mean ant abundance by treatment (patch size and use).

Species	Ant abundance	Mean abundance per site		
		Small–high ($N = 9$)	Large–high ($N = 10$)	Large–low ($N = 5$)
Aphaenogaster fulva	376	10.1[a]	19.0[b]	19.0[b]
Aphaenogaster rudis	75	7.9[a]	0.4[b]	0.0[b]
Camponotus pennsylvanica	38	3.8[a]	0.2[b]	0.4[a,b]
Camponotus chromaiodes	29	2.1[a]	0.9[a]	0.2[a]
Lasius alienus	12	0.6	0.7	0.0
Formica schaufussi	9	0.4	0.5	0.0
Lasius umbratus	3	0.3	0.0	0.0
Crematogaster cerasi	2	0.2	0.0	0.0
Crematogaster vermiculata	2	0.2	0.0	0.0
Myrmecina americana	2	0.2	0.0	0.0
Prenolepis imparis	2	0.0	0.2	0.0
Camponotus castaneus	1	0.1	0.0	0.0
Paratrechina melanderi	1	0.1	0.0	0.0
Total no. collections	552			

Note: Within rows, means with the same superscript letter do not differ significantly.

FACTOR procedure in SAS (1996) using a principal components solution and varimax rotation. The number of factors was determined by counting the number of principal components having eigenvalues >1.0. The rotated factor loadings were examined to assess the correlation structure of these data.

RESULTS

Effect of patch size and past land use on ant abundance and species richness

A total of 552 ant collections, including 13 different species were made from the 24 study sites (Table 2). Total ant abundance was greater at small–high than at large–low patches (ANOVA, $P = 0.039$; Fig. 2A). Ant species richness also varied among treatments (ANOVA, $P = 0.032$), with mean species richness higher in small–high than in large–low patches (Fig. 2B, $P = 0.01$).

Seed-dispersing ant species occurred in all study patches, but there were substantial differences in ant species composition among sites. Species within the genera *Aphaenogaster* and *Camponotus* (Hymenoptera: Formicidae) constituted ~94% of the total ant collections (Table 2). The combined total abundance of the four most numerous ant species, *Aphaenogaster fulva* (Roger) 1863, *Aphaenogaster rudis* (Emery) 1889, *Camponotus pennsylvanica* (DeGeer) 1773, and *Camponotus chromaiodes* (Bolton) 1995, was comparable among treatments ($P = 0.256$). However, large–low sites were dominated by one species, *A. fulva*, which accounted for 68% of all ants collected. Abundance of *A. fulva* was similar in large patches of either high or low past land-use intensity but was substantially lower in small–high patches. In contrast, *A. rudis* was collected much more frequently in small–high patches than in large patches of either past land-use intensity.
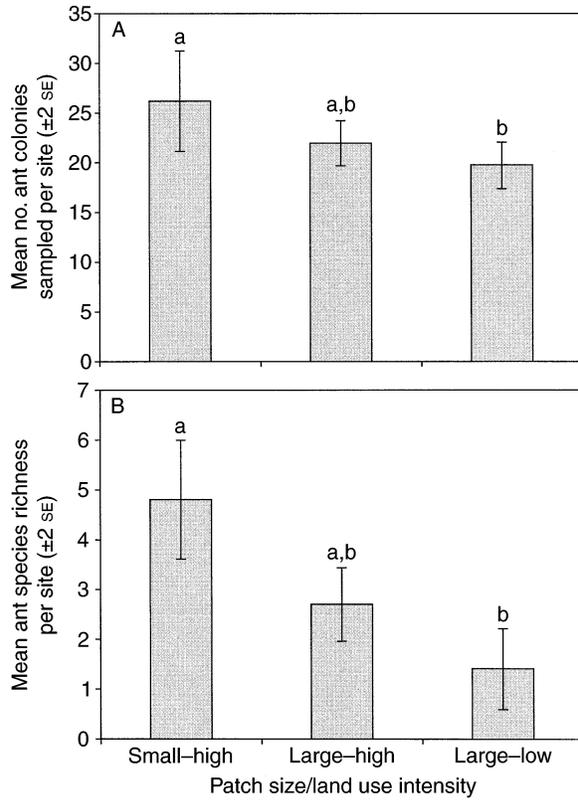
FIG. 2. (A) Mean ant abundance and (B) mean ant species richness sampled by patch-size/land-use treatment with 95% confidence intervals. Significant differences between treatments are denoted by letters that differ.

Camponotus species were more likely to be found in small forest patches. Significantly more *C. pennsylvanica* collections were made in small–high than large–high patches.

Effect of patch size and past land use on myrmecochore richness and abundance

Species richness of adult myrmecochores was greatest in large–low patches and lowest in the small–high treatment (Fig. 3). Richness of juvenile myrmecochores was lower than that of adults and did not vary among treatments. Sites in large–low and large–high patches supported higher richness of seedling myrmecochores than did the small patches ($P < 0.05$).

The abundance of myrmecochores also varied among treatments. Large–low patches supported the highest number of adults and small–high patches the least (Fig. 4A). Abundance of Liliaceae and *Viola* adults was greater at large–low sites compared to large–high and small–high sites. Abundance of immature myrmecochores was greatest at large–low sites and lowest at small–high sites (Fig. 4B). The abundance of immature lilies also varied between large–low and small–high patches, but abundance of immature violets did not vary among treatments.
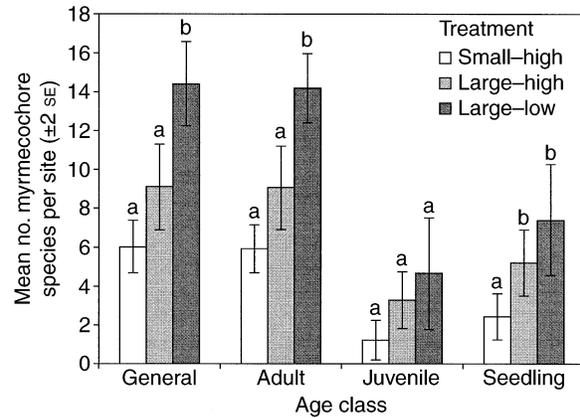

FIG. 3. Mean myrmecochore species richness for all age classes (general) and different age classes by patch-size/land-use treatment. Significant differences among treatments are denoted by letters that differ.

Explaining variability in ants and myrmecochores

There were correlations among the ant variables and among the treatment and plant variables (Mitchell 2000). Among the ant variables, ant abundance was
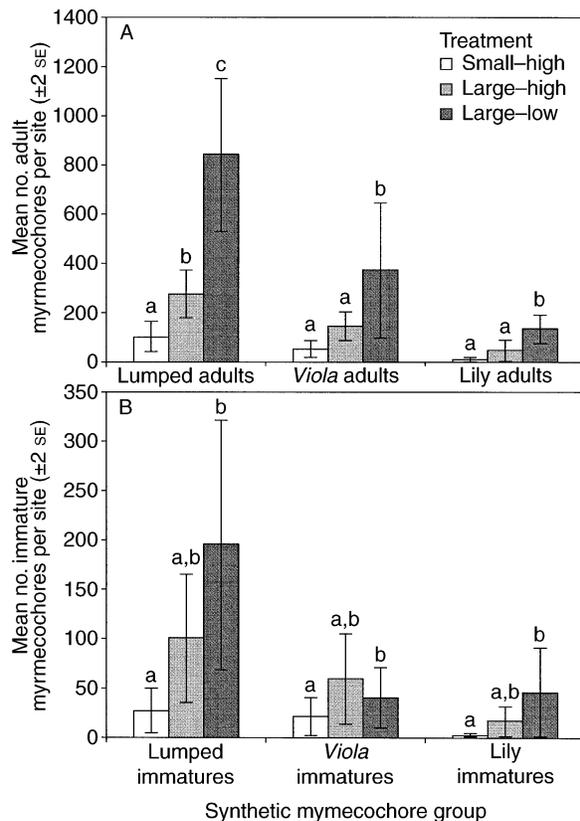

FIG. 4. Mean abundance of (A) adult and (B) immature synthetic myrmecochore groupings by patch-size/land-use treatment. Significant differences among treatments are denoted by letters that differ.

TABLE 3. Canonical correlation structure among ant variables, treatment, and adult myrmecochores at the site level.

A) Correlations among ants and their canonical variables

	Dependent no. 1	Dependent no. 2
Ant abundance	−0.91	−0.19
Ant species richness	−0.60	−0.43
A. fulva abundance	+0.78	−0.22
A. rudis abundance	−0.90	+0.37
Camponotus abundance	−0.59	−0.54

B) Correlations among adult plants and their canonical variables

	Independent no. 1	Independent no. 2
Treatment	+0.99	−0.16
Adult abundance	+0.92	+0.37
Adult lily abundance	+0.78	+0.24
Adult violet abundance	+0.73	+0.48

positively related to ant richness and the abundance of *A. rudis* and *Camponotus* spp. and negatively related to the abundance of *A. rudis*. The abundance of *A. fulva* was negatively related to the abundance of *A. rudis*, ant abundance, richness, and the abundance of *Camponotus* spp. Among the plant variables, the total number of adult plants, adult lilies, and adult violets were positively correlated with the patch size/land use treatments.

Canonical correlation analysis.—

1. *Ant model (ants = treatment + adult plants).*— Among sites, ant diversity and abundance were correlated with land use/patch size treatments and the abundances of adult plants. The first dependent canonical variable was strongly negatively influenced by ant abundance and the abundance of *A. rudis*, and positively by the abundance of *A. fulva* (Table 3). The second dependent variable showed similar correlations except that the correlations with the *Aphaenogaster* species were reversed. The first independent canonical variable was positively correlated with the treatment categories and abundances of adult plants of all species.

The strongest correlation for the second independent variable was with the abundance of adult violets.

Ant variables were correlated primarily with the first canonical variate of the independent variables (Table 4), which was strongly correlated with treatment and the abundance of adult plants (Table 3). For the second set of canonical correlates, ant richness and *Camponotus* species were negatively associated with the abundance of violet adults. Canonical correlations for the first two sets of variables were >0.70 (Wilks' lambda $F_{20,50} = 2.51$, $P = 0.004$; Table 4). Canonical redundancy analysis revealed that 42% of the variance in ants could be explained by the first canonical variate of independent variables. The explanatory power of the second independent variate was negligible (<8%). This analysis revealed that ant abundance and *A. rudis* abundance were greater in the small patches with high land-use intensity patches, whereas *A. fulva* abundance was greater in the large patches with low land-use intensity. *A. fulva* was more abundant at sites with higher abundances of myrmecochores while *A. rudis* was negatively correlated with myremecochore abundance.

Within sites (i.e., at the bait level), ant abundance and diversity were correlated with land use/patch size treatments and the abundance of adult plants. The first dependent canonical variate was correlated with increased abundance of *A. fulva*, lower ant richness, and lower abundances of *A. rudis* and *Camponotus* spp. The second dependent variate was correlated with lower ant richness, higher abundance of *A. rudis*, and lower abundances of *A. fulva* and *Camponotus* spp. Thus, these two variates distinguish between abundances of *Aphaenogaster* and *Camponotus*. The first independent canonical variate was highly correlated with treatment and adult plants. The second variate was associated with all adults and adult violets in particular. However, although the canonical correlation was statistically significant ($P < 0.001$), the explanatory power of these canonical variates was low for the ants, accounting for only 10% of the variance in ants. Overall, ant abundance was only weakly related to the abundance of myrmecochores within sites.

TABLE 4. Canonical redundancy analysis of ant variables, treatment, and adult myrmecochores at the site level.

	Ant canonical variables			Treatment and adult plant canonical variables	
Canonical correlation	Proportion	Cumulative proportion	Canonical R^2	Proportion	Cumulative proportion
1	0.59	0.59	0.72	0.42	0.42
2	0.14	0.73	0.55	0.08	0.50
3	0.13	0.86	0.20	0.03	0.53
4	0.03	0.89	0.003	0.0001	0.53

Notes: The numbers presented list the proportion of variation in the original ant variables explained by the dependent canonical variates (ant variables) and the independent canonical variates (treatment and adult plant variables). The canonical R^2 reflects the amount of variation in the dependent canonical variate that can be explained by its corresponding independent canonical variate.

TABLE 5. Canonical correlation structure between immature myrmecochores, treatment, ant variables, and adult myrmecochores at the site level.

A) Correlations among immature plants and their canonical variables

	Dependent no. 1	Dependent no. 2
Immature abundance	+0.51	+0.68
Immature lily abundance	+0.78	−0.12
Immature violet abundance	−0.07	+0.52

B) Correlations among ants and adult plants and their canonical variables

	Independent no. 1	Independent no. 2
Treatment	+0.72	+0.43
Ant abundance	−0.39	−0.34
Ant species richness	−0.23	−0.27
A. fulva abundance	+0.37	+0.25
A. rudis abundance	−0.46	−0.29
Camponotus abundance	−0.14	−0.30
Adult abundance	+0.56	+0.56
Adult lily abundance	+0.75	−0.04
Adult violet abundance	+0.13	+0.41

2. *Plant model (immature plants = treatment + ants + adult plants).*—Among sites, the abundance of immature plants was correlated with the abundance of conspecific adults and the abundance of *Aphaenogaster* species. The first dependent canonical variate was correlated with all immature plants and with immature lilies (Table 5). The second dependent variate was correlated with immature plants and with immature violets. The first independent canonical variate was strongly correlated with treatment, low ant abundance and diversity, increased abundance of *A. fulva*, lower abundance of *A. rudis*, increased abundance of all adult plants and lily adults. The second independent variate was correlated with treatment, lower ant abundance, increased abundance of all adult plants and adult violets. A similar distinction between adult lilies and violets was evident in the independent variables.

The first two canonical correlations in this analysis showed strong, statistically significant relationships among the canonical variates ($R > 0.85$, Wilks' lambda

$F_{27,35} = 4.47$, $P < 0.001$; Table 6). The first two independent canonical variates explained a total 46% of the variation in the abundance of immature plants. The results revealed that immature plants were most abundant at sites having greater abundance of mature conspecifics and greater abundances of *A. fulva*. Immature lilies were most abundant at sites with a large number of lily adults. Sites having greater abundances of immature plants also tended to have lower ant abundance and lower abundances of *A. rudis* and *Camponotus* spp. Based on the correlation structure of these data (Table 6), immatures were more strongly related to adult conspecifics than to ant abundance.

Within sites, the abundances of immature plants were correlated with land use/patch size and the abundances of conspecific adults. Correlations with ant variables were largely absent. As at the site level, the dependent canonical variates distinguish between immature lilies (first variate) and immature violets (second variate). The first independent canonical variate is correlated with treatment, all adults, and adult lilies. The second independent variate is correlated with treatment, all adult plants, and adult violets. The only strong relationship in the second canonical correlation was between violets and *Camponotus* spp. Each of the first two independent canonical variates explained ~15% of the total variation in immature plants.

ANOVA results: Complex relationships among ant and myrmecochore variables.—The results from ANOVA revealed relationships among the ant and plant variables that were not apparent in the canonical correlations. These results, summarized in Table 7, indicated that the patterns of correlation among ants and myrmecochores and between immature and mature myrmecochores were not uniformly consistent among the three patch size/land use categories of sites. These inconsistencies are summarized in the following two paragraphs. Only patterns that were not captured in canonical correlations are discussed.

At the site level, ant abundance was significantly correlated with the patch size/land use treatment and adult violets. However, the effect of violets was only apparent in the small patches where there was negative

TABLE 6. Canonical redundancy analysis of immature myrmecochores, treatment, ant variables, and adult myrmecochores at the site level.

Canonical correlation	Immature myrmecochore canonical variables		Canonical R^2	Treatment, ant, and adult plant canonical variables	
	Proportion	Cumulative proportion		Proportion	Cumulative proportion
1	0.30	0.30	0.93	0.27	0.27
2	0.25	0.55	0.73	0.18	0.46
3	0.46	1.00	0.30	0.13	0.59

Notes: The numbers presented list the proportion of variation in the original immature myrmecochore variables explained by the dependent canonical variates (immature myrmecochores) and the independent canonical variates (treatment, ants, and adult plants). The canonical R^2 reflects the amount of variation in the dependent canonical variate that can be explained by its corresponding independent canonical variate.

TABLE 7. Significant relationships among ant and myrmecochore variables.

Models
Site level
Ant abundance = treatment − violet adults*** + treatment × violet adults
Adult lily = treatment − ant richness + treatment × ant richness
Immature plants = −ant abundance + treatment × adult plants
Bait level
Ant richness = treatment*** + treatment × adult plants****
A. fulva abundance = treatment*** + treatment × violet adults
C. chromaiodes abundance = treatment − violet adults***
Adult violets = treatment − C. pennsylvatica activity + treatment × C. pennsylvatica abundance
Immature violets = violet adults*** + treatment × violet adults

Notes: The models listed were from a mixed ANOVA analysis. Models that are redundant with the results of the canonical correlation analysis are not listed. Only effects with $P \leq 0.01$ are listed (*** $P \leq 0.001$, **** $P \leq 0.0001$).

correlation between ant abundance and the abundance of violet adults. Adult lilies were correlated with treatment and negatively by ant richness; however, the effect of ant richness was manifest only at sites in large patches. There was no significant effect of ant richness in small patches. The abundances of immature plants were negatively correlated with ant abundance and show an interaction with treatment and adult plants. This interaction was due to correlations with adult plants that varied among patch size/land use treatments. There was no effect of adult plants in small patches, a positive effect in large–high patches, and a negative effect in large–low patches.

At the level of an individual bait station, relationships between the ant community and adult plants varied among treatments. Ant richness was negatively correlated with the abundance of adult plants but only at sites in the small patches. Abundance of *A. fulva* was positively correlated with the abundance of adult violets but only in large patches. There were similar sit-

uations with plant variables. Adult violets were less abundant at bait stations where *C. pennsylvatica* was present at sites with high levels of prior land use. In contrast, this relationship was positive at sites in the large–low patches. The abundances of immature violets were positively correlated with the abundance of adults around the bait station. However, the strength of this correlation varied among the patch size/land use treatments. The correlation was strongest in data from the small patches.

Differences in habitat characteristics among treatments

Several habitat characteristics differed among the patch size and land-use categories (Table 8). Canopy cover was high and did not differ among patches, but understory cover was greater in small–high patches than large–low patches. Elevation varied among treatments, with small patches occurring at a lower range of elevations in the study region compared to the larger

TABLE 8. Site means and standard errors for habitat measures including soil metrics, canopy and understory scores, and elevation.

Habitat measure	Patch-size–land-use		
	Large–low	Large–high	Small–high
Soil metrics			
Humic matter (%)	0.98 ± 0.10[a]	0.92 ± 0.08[a]	0.62 ± 0.04[b]
Mass : volume	0.72 ± 0.03[a]	0.75 ± 0.03[a]	0.83 ± 0.04[a]
Cation exchange capacity	15.4 ± 1.4[a]	12.4 ± 1.5[a]	8.50 ± 0.9[b]
Acidity (mmol/L)	2.0 ± 0.22[a]	2.4 ± 0.4[a]	2.0 ± 0.2[a]
pH	5.9 ± 0.19[a]	5.8 ± 0.2[a]	5.6 ± 0.2[a]
Phosphorous index level	2.2 ± 0.66[a]	12.3 ± 6.9[a]	12.7 ± 7.1[a]
Potassium index level	118 ± 16.7[a]	85.0 ± 8.7[b]	75.3 ± 9.7[b]
Calcium index level	70.6 ± 1.7[a]	56.6 ± 6.5[a,b]	50.4 ± 3.9[b]
Copper index level	112 ± 17.9[a]	67.6 ± 9.8[b]	27.7 ± 7.7[c]
Cover variables			
Canopy cover score	4.4 ± 0.07[a]	4.3 ± 0.06[a]	4.1 ± 0.06[a]
Understory cover score	1.0 ± 0.05[a]	1.2 ± 0.04[a,b]	1.4 ± 0.04[b]
Topographic variable			
Elevation (m)	1136 ± 31.5[a]	890 ± 26.4[b]	686 ± 13.0[c]

Note: Among treatments, means with the same superscript letter do not differ significantly.

patches. Humic matter and cation exchange capacity were significantly lower in small patches than large patches of either past land-use intensity. Potassium index levels were highest in the large–low patches and significantly lower in patches with high-intensity past land use. Calcium and copper index levels also varied among treatments and were highest in the large–low patches. In contrast, phosphorus index level was nearly six times greater in patches with past land use than in the large–low patches. Sites in large–low patches had a higher calcium index level than small–high patches.

DISCUSSION

Ant species richness and abundance

Ant species richness and ant abundance did vary among the mesic forest patches that we sampled, but the relationship was not as we predicted. As suggested by previous studies (Pudlo et al. 1980, Andersen 1986, Crist and Wiens 1994, Roth et al. 1994, Suarez et al. 1998), we expected that anthropogenic disturbance would negatively impact ant abundance and diversity. Most ant societies are highly dependent on the structure, moisture, and temperature of the soil (Levings 1983, Puntilla et al. 1991), so prior land use and edge effects related to patch size (Matlack 1993) could influence microenvironmental factors and, in turn, the number and diversity of ants. Native ant species may be more abundant away from edges and in areas with predominantly native vegetation (Suarez et al. 1998), suggesting that edge effects can reduce the ability of smaller patches to retain native ant species. Reduction or elimination of seed dispersing ant species can alter the demography of plant populations, resulting in adult populations simply awaiting extirpation because of the lack of seedling recruitment (Pudlo et al. 1980).

In contrast to our predictions, we observed that ant abundance and species richness were greater in small patches with histories of more intense land use and lower in large patches with minimal past land use. Our findings suggest that A. fulva, which was the dominant species in the large–low patches, may be more tolerant of shade than A. rudis or Camponotus. Aphaenogaster species are nonterritorial generalists, with a very broad ecological niche in regard to nest placement, food specialization, mobility, and seasonal activity (Beattie et al. 1979, Lynch et al. 1980). However, A. fulva prefers mesic conditions (Talbot 1934, Cole 1940, Headley 1949, Carroll 1975) and may be the only abundant ant found in deep woods, and even swamps, where there is a constancy of conditions and lack of habitat variety (Talbot 1934, Cole 1940). Cole (1940) identified A. fulva as being somewhat rare in the Great Smoky Mountains but well distributed among favorable habitats. These trends are consistent with the increased abundance of A. fulva we observed in the large–low patches. There were no significant differences in tree canopy cover among our sites, but the increased ground-level herbaceous cover in large–low sites would limit the amount of sunlight reaching ant nest sites (Puntilla et al. 1991). Ant colonies tend to move away from patches of forest floor that are deeply shaded by vegetation, probably because temperatures were insufficient for brood development (Smallwood 1982). Many ant species have narrow limits of tolerance, with the establishment and persistence of a given ant species in an area dependent on the availability of suitable food and nest sites and the strength of competitors and predators (Levings 1983).

The greatest differences due to patch size and land use were manifest in ant community composition. The increased abundances of Camponotus spp. and A. rudis in small patches may be related to microhabitat differences related to edge effects and elevation. The small patches generally occurred at lower elevations and would be warmer and drier than sites in the large patches. Ants in the southern Appalachians are usually most abundant at elevations from 450–600 m (Cole 1940), and the number of ant species decreases with increasing elevation. Aphaenogaster species are common from low to high elevations (up to 1500 m), but species in this genus vary in optimum elevation ranges. Camponotus species are less common in the region but are more abundant at lower elevations and scarce at elevations >1200 m. Camponotus species favor well-insolated habitats and are most abundant and diverse in more arid habitats (Talbot 1934, Andersen 1991). This is unusual because dry conditions are generally unfavorable to ants (Levings 1983). Most sources also describe Camponotus as being primarily nocturnal (Sanders 1972, Lynch et al. 1980); however, we encountered few Camponotus species compared to Aphaenogaster species during our nocturnal sampling. However, our overall findings are consistent with previously described behaviors and habitats of the ant species.

Ant diversity and abundance were related to land use/patch size and the abundance of adult myrmecochores at both scales of analysis (among sites and within sites). However, the explanatory power of the relationship was greater among sites and relatively weak within sites, suggesting the importance of broadscale factors in influencing ants. In general, myrmecochore variables explained differences in ants better than ant variables explained differences in myrmecochores.

The main seed-dispersing ant species (A. fulva, A. rudis, C. chromaiodes, and C. pennsylvanica) we observed differ in behavior, and this may help explain patterns of both ants and myrmecochores. A. rudis is a very common diaspore-carrying species in the eastern United States (Handel 1976, Beattie and Culver 1978, Beattie et al. 1979, Lynch et al. 1980, Heithaus 1981, Smallwood 1982, Fellers 1987, Morales and Heithaus 1998). A. fulva is referenced less in the literature, perhaps because of a long history of nomenclatural confusion among the morphologically similar Aphaeno-

gaster rudis/texana group of species (Carroll 1975). Many studies (e.g., Headley 1949, Lynch et al. 1980) emphasize the effectiveness of *Aphaenogaster* species at removing diaspores, with 50% of available seeds removed within only 30 min (Beattie et al. 1979). *Aphaenogaster* species were more efficient in locating baits than *Camponotus* species (C. E. Mitchell, *personal observation*), similar to findings of other studies (Lynch et al. 1980, Fellers 1987). *Aphaenogaster* species are also very efficient at handling seeds, and they use tools to aid in carrying large objects (Culver and Beattie 1978). In habitats such as the southern Appalachians, where seed predation by rodents can be high (Heithaus 1981) and nutrients are monopolized by dominant tree stands, escape from predators and nutrient enrichment may be key advantages offered by myrmecochory (Beattie 1985). Ant nests may be particularly favorable nutrient-enriched microsites (safe sites) for germination and seedling emergence and establishment (Beattie and Culver 1980, Andersen 1988*a*). Furthermore, diaspores dispersed by ants may have reduced parental and seedling competition (Beattie and Culver 1981, Kjellsson 1991, Gomez and Espalder 1998). An abundance of *Aphaenogaster* workers, such as we observed in large–low patches, might reduce rodent predation on seeds and enhance diaspore dispersal.

In contrast, the relatively large *Camponotus* species have longer dispersal distances (2.26 m, compared to only 0.69 m for the smaller myrmicines, which includes *Aphaenogaster* (Gomez and Espalder 1998). *Camponotus* species may also be able to disperse larger seeds given their greater body size. *Aphaenogaster* species located baits more quickly, but the larger ant species (i.e., *Formica* and *Camponotus*) dispersed tuna back to their nests much more rapidly. Formicines often depleted baits in less than an hour, while myrmicines never removed a significant amount of tuna from baits even after an entire day. However, *Camponotus* species, commonly known as carpenter ants, primarily nest in logs and stumps (Talbot 1934, Cole 1940). Many *Camponotus* workers dispersed tuna into the canopy of nearby standing trees suggesting that seeds might similarly be dispersed to inappropriate germination sites. In addition, *Camponotus* workers have large, powerful mandibles, and some diaspores may be broken and eaten in full by these ants. Therefore, a shift in the ant community from one dominated by *Aphaenogaster* to one dominated by a combination of *Aphaenogaster* and *Camponotus* could have negative consequences for myrmecochores. Because of the high probability of seed removal within short periods of time (Hughes and Westoby 1990), it is unlikely that seed dispersal is limiting for myrmecochores. However, successful germination and even survival may depend on which ant species removes the seeds (Hughes and Westoby 1992*b*).

Competitive interactions also may influence observed ant community composition. Scramble and territorial (interference) competition among ant colonies occurs largely for nest sites and food for young or mature colonies (Carroll and Janzen 1973). One might expect an inverse relationship between dominance (interference interactions) and relative speed with which baits are found (Fellers 1987). Formicine ants generally dominate myrmicine ants (Fellers 1987), and competitive interactions in the small–disturbed patches were dominated by the larger *Camponotus* species. A single *Camponotus* worker could protect a tuna bait from a mass of *Aphaenogaster* workers hovering around a bait (C. E. Mitchell, *personal observation*), similar to observations made by Lynch et al. (1980) and Fellers (1987). *C. chromaiodes* and *C. pennsylvanica* are both highly aggressive species and could exert a strong negative influence on feeding activity and seed removal rate of *Aphaenogaster* species (Lynch et al. 1980). In addition, *Aphaenogaster* abundance might actually be higher in small patches than our sampling indicated if *Camponotus* monopolized the baits.

Myrmecochore species richness and abundance

Myrmecochores were negatively related to land-use intensity and positively related to patch size, as expected (Pearson et al. 1998). Land-use history rather than patch size accounted for the greatest differences among the sites, and most ant variables (e.g., abundance, richness) were not important. Higher abundance of *A. fulva* was associated with a greater abundance of myrmecochores, but greater densities of immature myrmecochores occurred with higher numbers of conspecific adults only in patches with high past land use. Therefore, past extirpation of adult myrmecochores, combined with short dispersal distances for expansion of existing adult populations, may be responsible for the lower abundances of these plants in areas that experienced high-intensity land use in the past. Our results suggest that myrmecochores can recruit into disturbed forest patches if mature, seed-producing plants are present.

The abundance of immature myrmecochores was related to the abundance of conspecific adults among sites and within sites, as we hypothesized. Among ant variables, abundance of *Aphaenogaster* species was correlated with the abundance of immature myrmecochores at the site level. Thus, our results suggest that broadscale factors are influencing both ant and myrmecochore distributions.

Beattie and Culver (1981) found ant abundance to be a good positively correlated predictor of the number of myrmecochorous species at a given site. However, we observed a negative correlation between ant abundance and species richness and myrmecochore abundance and diversity (Fig. 5). Our results suggest dispersal of seeds by ants is still available in small, disturbed patches; the absence of seed-dispersing ants cannot explain the reduced numbers of myrmecochores
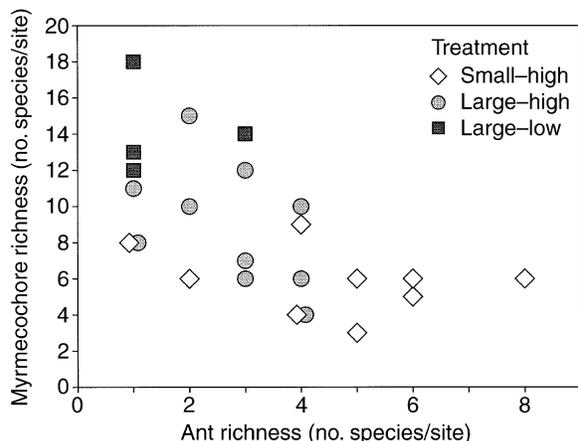
Fig. 5. Myrmecochore species richness vs. ant species richness among sites.

observed in the small patches with high past land use. Small patches with high past disturbance supported a great abundance and diversity of ants, suggesting again that the effects of land-use legacies or fragmentation on microhabitats may override any advantages offered by ants to myrmecochores. However, the positive relationship between myrmecochorous species and *Aphaenogaster* abundance suggests that ant species composition may be more important for myrmecochores than ant diversity. Thus, the loss of *Aphaenogaster* species in small forest patches may be related to the loss of plant diversity.

It is possible that *Aphaenogaster* species may be more effective than other ant taxa at locating and dispersing actual seeds, rather than tuna baits. The spatial dispersion of tuna baits is also likely to be different that the dispersion of seeds, and although this technique is appropriate because of the diglyceride linkage to the elaisomes, ant responses to seeds may still differ. If elaisome-bearing seeds were used instead of tuna baits, a smaller subset of the overall ant community might have been recorded.

Conclusions

Land-use history and habitat fragmentation may influence the future persistence of myrmecochores in the southern Appalachians. Duffy and Meier (1992) predicted that vernal understory recovery might take >100 yr, and may never return to primary conditions. Intrinsically low rates of reproduction and slow growth of herbs and degradation of suitable habitat retard recovery (Meier et al. 1995). Recolonization of suitable sites by myrmecochores within patches will be slow, and gaps between forest patches may greatly retard dispersal among patches. However, the abundance of juvenile myrmecochores in patches with high past land use increased if adult conspecifics were present. This suggests that the reintroduction of adult myrmecochores into patches from which they are now absent

might be effective for initiating local reproduction and dispersal. Because habitat characteristics, especially soil nutrients and humic matter, differed among treatments, transplant experiments should be conducted to ascertain site suitability for myrmecochores and to determine whether recruitment is indeed catalyzed.

Plant–animal mutualisms such as myrmecochory play critical roles in maintaining ecological function and offer ecologists an opportunity to increase understanding of community processes (Beattie 1985, Andersen 1991). Further studies of myrmecochory in the southern Appalachians should address factors such as ant competition, seed selectivity by ant species, removal rates of seeds by ants, dispersal destinations, and rodent predation. In addition, the influence of historic land use on soil attributes and biogeochemical cycling should be studied further. Finally, conservation of invertebrates demands greater attention because of the critical ecosystem processes, such as seed dispersal, that they support (Wilson 1987, Franklin 1993, Dale et al. 1994, Andersen 1997, Folgarait 1998).

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