

Rarity and Diversity in Forest Ant Assemblages of Great Smoky Mountains National Park

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Abstract - We report on a systematic survey of the ant fauna occurring in hardwood forests in the Great Smoky Mountains National Park. At 22-mixed hardwood sites, we collected leaf-litter ant species using Winkler samplers. At eight of those sites, we also collected ants using pitfall and Malaise traps. In total, we collected 53 ant species. As shown in other studies, ant species richness tended to decline with increasing elevation. Leaf-litter ant assemblages were also highly nested. Several common species were both locally abundant and had broad distributions, while many other species were rarely detected. Winkler samplers, pitfall traps, and Malaise traps yielded samples that differed in composition, but not richness, from one another. Taken together, our work begins to illuminate the factors that govern the diversity, distribution, abundance, and perhaps rarity of ants of forested ecosystems in the Great Smoky Mountains National Park.

Introduction

Robert Whittaker's (1952, 1956) classic work showed that the elevational gradient in the Great Smoky Mountains National Park (GSMNP) strongly influences plant and insect communities. Since Whittaker's work, few studies (see Stiles and Coyle 2001, Van Pelt 1963, Watson et al. 1994) have explored elevational gradients in diversity in the southern Appalachians. As for most taxa, ant diversity often varies systematically along elevational gradients (Brühl et al. 1998; Fisher 1996, 1998; Olson 1994; Sanders 2002; Sanders et al. 2003), but no studies to date have explicitly examined elevational gradients in ant diversity in the southern Appalachians.

At least two early investigators focused on the ant fauna of the southern Appalachians. First, Cole (1940) performed one of the earliest ant surveys of any National Park and one of the first systematic surveys of any taxon in the GSMNP (though he focused only on the Tennessee side of GSMNP). Cole (1940) thoroughly inventoried the ant fauna of the GSMNP and provided notes on the distribution and autecology of the species he observed in his forays. Second, Van Pelt (1963) studied the ant communities of the southern Blue Ridge Mountains with a particular interest in the variation in regional

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patterns of ant diversity and community composition at low and high-elevation sites. These early studies by Cole and Van Pelt provide contemporary ecologists with a unique knowledge of the history of ant assemblages in the southern Appalachian Mountains.

Because of the ecological importance and near ubiquity of ants in most terrestrial ecosystems (Hölldobler and Wilson 1990), understanding the causes and consequences of ant diversity is critical to preserving both ecosystem functions and services that ants provide (Folgarait 1998). As part of the All Taxa Biodiversity Inventory (ATBI; [Sharkey 2001]), we have sought to understand the biotic and abiotic controls on ant diversity. Our goals in this paper are to: (i) estimate litter ant species richness at 22 forest sites in the GSMNP; (ii) document the major spatial patterns in the diversity, distribution, and abundance of ants in the GSMNP; (iii) assess whether ant assemblages are nested, where nestedness is a measure of the extent to which species-poor assemblages are subsets of species-rich assemblages; and (iv) examine how different sampling techniques yield different components of ant assemblages. To accomplish the first three goals, we used data from leaf-litter ant assemblages collected at 22 sites during 2004 and 2005. To accomplish the fourth goal, we used a combination of different sampling techniques (pitfall traps, Malaise traps, and Winkler extractors) to inventory ant workers and alates at eight sites in the GSMNP.

Methods

Sampling

We collected ants at 22 forested sites using Winkler extractors in 2004 and 2005. At eight of those 22 sites, we also collected ants using pitfall traps and Malaise traps as part of C. Parker's "ATBI Pilot Study." The 22 sites were chosen to cover nearly the entire range of elevation in the GSMNP (260–2021 m). Our sampling design ensured that about 80% of the elevational range in the GSMNP was sampled. Sites were chosen on both the NC and TN side of the GSMNP, and from the southern to the northern boundaries of the park (Fig. 1). All sites were located in mixed-hardwood forests, which is the main forest type found throughout the park (White 1983), and all sites were located away from roads, heavily visited trails, or other human disturbances.

Leaf-litter ant sampling (Winkler Extraction). At each of the 22 sites described above, we randomly placed a 50-m x 50-m plot. Within the corners of this plot, we placed a 10-m x 10-m sub-plot, and within the corners of each 10-m x 10-m sub-plot, we sampled ants in four 1-m² plots. Thus, at each site, there were 16 1-m² plots. We collected the leaf litter inside each 1-m² plot and sifted it through a coarse mesh screen of 1-cm grid size to remove the largest fragments and concentrate the fine litter (see Longino and Colwell 1997, Longino et al. 2002). The litter fragments that did not fit through the mesh, twigs, and sticks in each 1-m² plot were inspected for colonies. The concentrated fine litter from each sample was then suspended

in mini-Winkler sacks for two days in the lab. All worker ants that were extracted from the 1-m² plots were identified and enumerated and are stored in Sander's ant collection at the University of Tennessee.

Pitfall trapping. We used pitfall traps to sample ants at eight forested sites (Table 1) within the GSMNP every two weeks from October 2000 through April 2003. At each of the eight sites, ten pitfall traps were placed at least 3 m apart along an approximately 30-m transect. Traps were 6-cm diameter plastic cups buried flush with the soil surface and partially filled with propylene glycol. Pitfall traps effectively capture ground-foraging ants (Bestelmeyer et al. 2000), while not always capturing those that are exclusively litter-dwelling species.

Malaise traps. Two Malaise traps (1.6 m × 1.8 m × 1.0 m) were placed on the ground 75–100 m from one another at each of the eight sites at which pitfall traps were placed (Longino and Colwell 1997, Longino et al. 2002). The contents of the alcohol-filled traps were collected every two weeks from January 1999 through January 2002.

Analyses

For each site and sampling technique, the observed number of species is simply the tally of species collected at the site. We examined how species richness (the total number of ant species occurring at a site) varied with elevation. To estimate species richness, the number of species that would be collected if sampling were to go to completion, we used the Chao2 estimator (Chao 1987, Colwell and Coddington 1994) as:

$$S_{\text{Chao2}} = S_{\text{Obs}} + Q_1^2 / 2Q_2,$$

where S_{Obs} is the number of species that occurred in the sample, Q_1 is the number of species that occur in only one sample (uniques), and Q_2 is

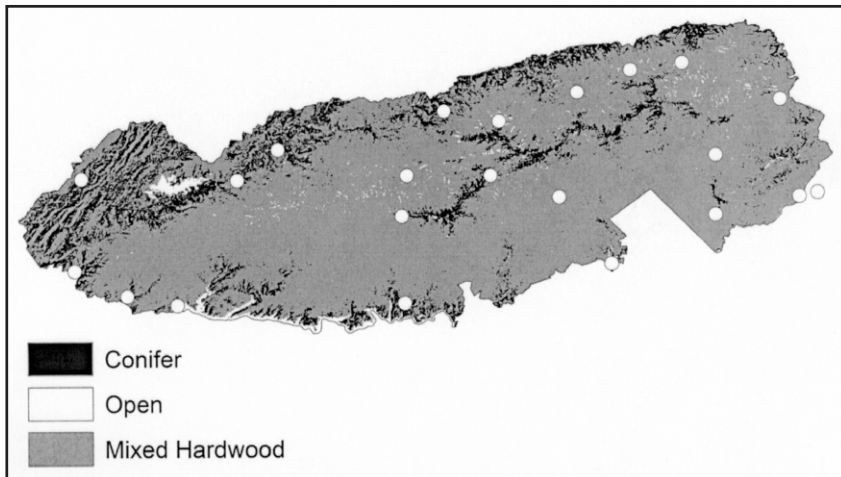


Figure 1. Map of the Great Smokies National Park (GSMNP) showing the 22 sites (white dots) where leaf-litter ants were sampled. The shadings represent the repartition and proportion of the main habitat-cover types in the GSMNP.

Table 1. Minimum and maximum elevation and number of sites occupied for forest ant species sampled in Great Smoky Mountains National Park. The elevation records are based on 8 sites for which data for the three different sampling techniques (malaise, pitfall, and Winkler sacks) were available. The number of occurrences are shown for each of the sampling techniques.

Species	Elevation (m)		Pitfall	Winkler	Malaise
	Min	Max			
<i>Amblyopone pallipes</i> (Haldeman)	594	1530	5	5	6
<i>Aphaenogaster fulva</i> Roger	594	1530	3	1	0
<i>A. lamellidens</i> Mayr	1530	1530	1	0	0
<i>A. rudis</i> Enzmann	594	1673	6	7	6
<i>A. sp.</i>	594	1380	0	0	2
<i>Brachymyrmex depilis</i> Emery	594	896	2	0	0
<i>Camponotus americanus</i> Mayr	594	594	0	0	1
<i>C. chromaiodes</i> Bolton	594	1033	4	0	4
<i>C. mississippiensis</i> Smith	594	594	0	0	1
<i>C. nearcticus</i> Emery	594	1380	1	0	3
<i>C. pennsylvanicus</i> (De Geer)	594	1530	3	1	5
<i>C. snellingi</i> Bolton	594	594	0	0	1
<i>C. subbarbatus</i> Emery	594	594	0	0	1
<i>Crematogaster ashmeadi</i> Mayr	594	594	0	0	1
<i>C. pilosa</i> Emery	594	1673	1	0	1
<i>C. sp.</i>	594	594	0	0	1
<i>Cryptopone gilva</i> (Roger)	594	896	2	0	0
<i>Formica subsericea</i> Say	594	994	0	0	2
<i>Lasius alienus</i> (Foerster)	594	1673	3	5	4
<i>L. latipes</i> (Walsh)	594	1530	0	0	2
<i>L. nearcticus</i> Wheeler	594	594	1	0	0
<i>Monomorium minimum</i> (Buckley)	594	594	0	0	1
<i>Myrmecina americana</i> Emery	594	1530	6	5	5
<i>Myrmica latifrons</i> Cole	594	896	0	0	2
<i>M. pinetorum</i> Wheeler	594	896	2	0	2
<i>M. punctiventris</i> Roger	594	1673	2	2	2
<i>M. sp.</i>	594	594	0	0	1
<i>Paratrechina sp.</i>	594	594	0	0	1
<i>P. sp.1.</i>	594	594	0	0	1
<i>Ponera pennsylvanica</i> Buckley	594	1673	3	2	4
<i>Prenolepis imparis</i> Emery	594	1530	4	1	2
<i>Proceratium croceum</i> (Roger)	594	594	0	0	1
<i>P. pergandei</i> (Emery)	594	594	0	0	1
<i>P. sp.</i>	594	594	0	0	1
<i>P. sp.1</i>	594	594	0	0	1
<i>Pyramica ohioensis</i> (Kennedy & Schramm)	594	594	0	1	0
<i>P. ornata</i> (Mayr)	594	594	1	0	0
<i>P. rostrata</i> (Emery)	594	594	0	1	0
<i>P. sp.</i>	594	594	0	0	1
<i>Solenopsis molesta</i> (Say)	594	1033	2	0	1
<i>Stenamma brevicorne</i> (Mayr)	594	1530	5	3	0
<i>S. diecki</i> Emery	594	1673	7	6	1
<i>S. impar</i> Forel	1033	1530	1	1	0
<i>S. meridionale</i> Smith	594	1673	6	5	0
<i>S. schmittii</i> Wheeler	594	1673	5	3	0
<i>S. sp.</i>	594	594	0	0	1
<i>S. sp.1</i>	994	1530	0	0	3
<i>S. sp.2</i>	594	1673	0	0	7
<i>Tapinoma sessile</i> (Say)	594	1530	0	0	2
<i>Temnothorax curvispinosus</i> Mayr	594	1033	0	0	3
<i>T. longispinosus</i> Roger	594	1380	2	1	4
<i>T. sp.</i>	594	1033	0	0	2
<i>T. sp.1</i>	1380	1380	0	0	1

the number of species that occur in two samples (Colwell and Coddington 1994). The Chao2 index uses data on the rare species collected in the samples (Q_1 and Q_2) to estimate the number of additional species that are present at the site, but were not recorded in the samples. As in other biodiversity studies of this kind, (Colwell et al. 2004, Kaspari et al. 2000, Longino et al. 2002, Ratchford et al. 2005), we treated each sampling unit (a 1-m² quadrat for the Winkler sampling or a pitfall trap for the pitfall trapping) as a sample. Because the Chao2 estimator is sensitive to sample size (Colwell and Coddington 1994), we used Colwell's EstimateS (Colwell 2004) to construct 50 randomized accumulation curves for each site to calculate the standard deviation of the estimated species richness. Across all sites, the asymptotic richness estimator was very similar to the observed total species richness ($r^2 = 0.64$, $p < 0.001$), and sampled diversity reached a plateau at all but two sites. Therefore, for ease of interpretation, we report only the observed richness for each site and sampling technique.

Elevational gradient. To examine whether leaf-litter ant diversity varied systematically with elevation, we plotted observed species richness from the Winkler samples from 22 sites against elevation. We assessed the relationship using linear regression.

Nestedness and rarity. We conducted two analyses to understand the distribution of rare ant species in the GSMNP hardwood forests: a nestedness analysis and a simple correlation between the diversity of rare ants and overall diversity. Nestedness analyses provide a measure of the extent to which the species found at species-poor sites are exclusive of or a subset of those found at species-rich sites. If sites are nested, those species at species-poor sites are a subset of those at species-rich sites. If sites are not nested, then species at species-poor sites are not necessarily found in species-rich sites. We performed an analysis of community nestedness using a presence/absence matrix comprising 22 sites and 38 species detected in the leaf-litter ant sampling. Nestedness can be assessed using the "nestedness temperature calculator" (NTC) implemented by Atmar and Patterson (1995). The NTC provides a T value between 0 and 100 describing the degree of nestedness of a given set of communities. A T value close to 0 is highly nested (where species at less diverse sites are strict subsets of those at more diverse sites), whereas a T value near 100 describes a random assemblage. The NTC further allows testing for statistical significance by generating 50 random matrices based on the original data set. The mean T value produced in the process is then compared to the observed T value and used to calculate a confidence interval. As an additional test of the distribution of rare ant species in the GSMNP forests, we looked at the correlation between the diversity of rare species (defined as those species found at no more than 4 sites) and overall ant diversity. In many regions, the diversity of rare species and overall diversity do not co-vary (Jetz et al. 2004), and as a consequence, conservation of diversity *per se* will not necessarily conserve those species most at risk.

Abundance and distribution. We examined the shape of the abundance-distribution curve by ordering species' frequencies of occurrence (the number of times they were detected) in litter samples, from the most rare to the most common species. This allowed us to illustrate the relative proportion of rare and common species in our litter samples. Then, to test whether abundant ants also tend to be widespread within the GSMNP forests, we regressed the number of occurrences (the number of 1-m² plots in which a species was detected) against the number of sites (out of 22) at which it was detected. If many species were uniques and/or singletons, it would be an indication that sampling at the scale of the park was relatively incomplete even though sampling in individual sites seemed relatively complete (see above).

Comparing sampling techniques. To compare the three sampling techniques (Winkler samples, pitfall traps, and Malaise traps), we first asked whether the number of species collected by one technique was correlated with the number of species collected by the other two techniques at the eight sites at which each of the three sampling techniques were employed. Then, to assess the similarity in composition of the assemblages sampled with each technique, we used the Jaccard's similarity index. The comparison was limited to the 8 sites where all three sampling techniques had been used.

Results

Leaf-litter ant assemblages. In total, we detected 38 leaf-litter ant species at the 22 sites. The number of species per m² ranged from 0–10, and the number of species per site varied from 2–22. In 20 of the 22 sites, the estimators reached an asymptote, indicating that further sampling would have added no new species. Leaf-litter ant species richness declined significantly with increasing elevation (Fig. 2, $r^2 = 0.63$, $p < 0.001$).

Nestedness and rarity. The 22 litter-ant assemblages sampled were nested ($T = 18.37^\circ$). The NTC randomization process generated 50 matrices that had an average T value of $62.2 \pm 4.11^\circ$. The original matrix had a significantly lower temperature than the mean T for the simulated matrices ($p = 2.64e^{-26}$), indicating that species-poor assemblages were composed of a subset of species-rich assemblages. The core species of most assemblages were *Aphaenogaster rudis*, *Myrmecina americana*, *Stenammas diecki*, *S. meridionale*, *Lasius alienus*, *Amblyopone pallipes* and *Ponera pennsylvanica* (Fig. 3). The diversity of rare species was well correlated with overall diversity, such that the most diverse sites had the most rare species (Pearson $r = 0.87$, $p = 0.001$).

Abundance and distribution. The species abundance distribution was approximately log normal, with a few common species and a tail of rare species (Fig. 4a). The abundance of individual species (the number of 1-m² plots a species was detected in) increased with the number of sites they occupied (Fig. 4b, $r^2 = 0.74$, $p < 0.0001$). One "species," *A. rudis*, represented a large percentage of all occurrences. *Aphaenogaster rudis* is likely a group of species rather than a single species (Umphrey 1996), but distinguishing

species within the group is possible only by examining their karyotypes. Regardless, the *A. rudis* species group appears to be tremendously successful in the southern Appalachia, a success that warrants further examination.

Pitfall and Malaise samples. Our inventory of the eight ATBI sites yielded a total of 15,340 ant individuals and 53 species, all sampling techniques (Winkler + pitfall + Malaise traps) combined (Table 1). Malaise traps at the same eight sites captured 30 species and over 10,000 alates; pitfall traps captured 25 species and 2796 workers; and litter samples yielded 17 species and 2242 workers. Due to the limited availability of taxonomic work on ant alates, we identified them to morphospecies and tried to be as conservative as possible in splitting species to avoid inflating the count of the number of species. We expect this conservatism to cause only a slight, if any, increase in the number of species recorded, and thus no significant effect on the relative species richness yielded by the different sampling techniques.

Comparing sampling techniques. To assess whether different sampling techniques provide equivalent estimates of the number of species sampled at our sites and the overall pattern of diversity, we correlated the different measures of species richness with one another. Measures of observed species richness were positively correlated to each other (Table 2). The

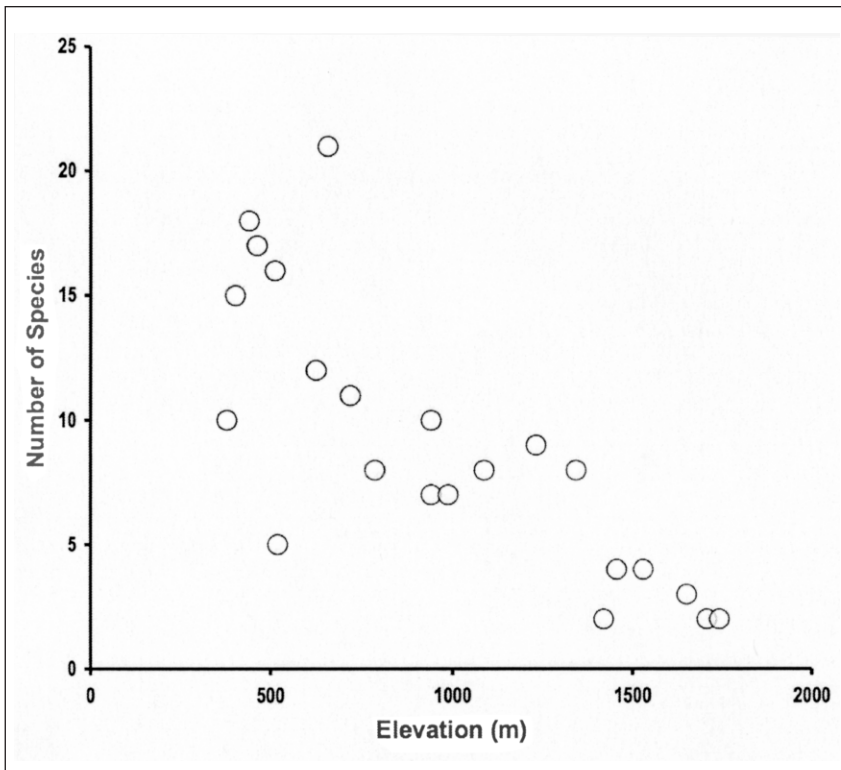


Figure 2. Elevational gradient in leaf-litter ant species richness for 22 sites surveyed during summer 2004–2005 in the Great Smokies National Park.

myrmecofauna collected with pitfall traps and Winkler extractors were similar to one another, but the fauna detected in the Malaise traps differed markedly from the faunas collected in Winkler extractors and pitfall traps (Table 3).

Discussion

To our knowledge, our work is the first systematic sampling of the ant fauna in the GSMNP. As with other taxa in the GSMNP (e.g., Whittaker

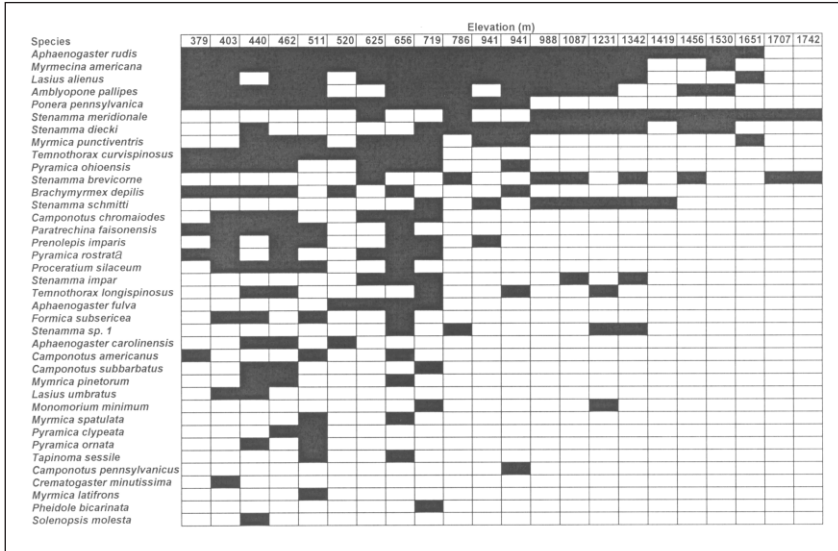


Figure 3. Presence/absence matrix of forest ant species illustrating the nestedness pattern of the 22 leaf-litter ant assemblages. Species are sorted from top to bottom by the number of sites they occupy.

Table 2. Correlation coefficients showing relationship between richness detected by three sampling techniques.

First sample	Second sample	Correlation coefficient	P
Pitfall traps	Winkler samples	0.835	0.010
Pitfall traps	Malaise traps	0.878	0.004
Winkler samples	Malaise traps	0.847	0.008

Table 3. The similarity in species composition among assemblages collected with three sampling techniques. Jaccard's values near 1 indicate more similarity, and values near 0 indicate less similarity.

First sample	Second sample	Jaccard similarity index
Pitfall traps	Winkler samples	0.703
Pitfall traps	Malaise traps	0.480
Winkler samples	Malaise traps	0.392

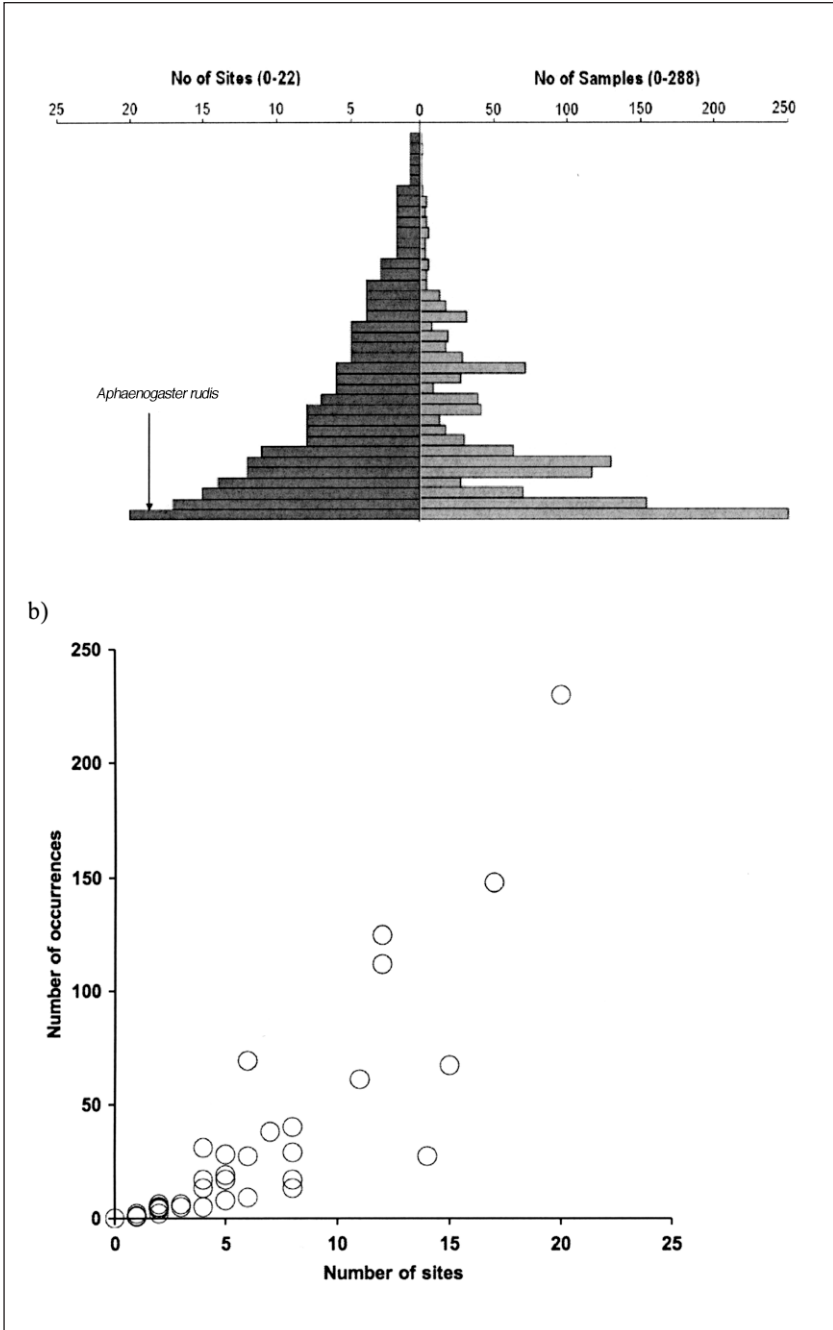


Figure 4. a) Species abundance distribution in 22 sites (black lines) and 288 one-m² plots of leaf-litter samples, and b) correlation between the relative abundance of leaf-litter ant species detected and the number of sites at which they occur.

1952), elevation strongly influenced leaf-litter ant diversity. Ant species richness decreased monotonically with elevation, a common pattern for many insect elevational diversity gradients (Rahbek 2005). Our results support the observations made by Van Pelt (1963), who found a greater number of ant “forms” and “nests” at lower elevations in the Blue Ridge mountains than at higher elevations. Similarly, Wang et al. (2001) found that ant species richness decreased with elevation in an oak forest of the central Appalachians. A regional faunistic survey of the ants of Georgia (Ipser et al. 2004) also found that ant species richness generally declined with elevation. Of course, the ants do not really respond to elevation per se. Instead, they respond to some biotic (e.g., productivity) or abiotic (temperature, geometric constraints) variable that covaries with elevation. The next step in our work in the GSMNP is to understand the biotic and abiotic factors that shape both spatial and temporal gradients in diversity (Dunn et al. 2007).

Leaf-litter ant assemblages in the GSMNP are highly nested. Species-poor assemblages (generally at the highest elevations) are made up of a subset of those species that occur at the most species-rich assemblages (generally at the lowest elevations). As a consequence, the diversity of rare species tracked the overall pattern of diversity. Ellison et al. (2002) calculated a T value of 15.1 for the bog ant assemblages in New England, comparable to the value we observed here. The ant fauna of the New England bogs is characterized by a few “bog specialists;” here we find a few low-elevation specialists.

In our study, ant species collected at the high-elevation sites were widely distributed across the elevational gradient surveyed, whereas the distributions of low-elevation species were often restricted to a few low-elevation sites. *Aphaenogaster rudis*, *M. americana*, *P. pennsylvanica*, and *S. dieckii* were widely distributed along the elevational range covered by our study. The most frequently collected ant species, *A. rudis*, was abundant within plots, common across multiple plots within sites and found at most sites in the GSMNP, while others species were represented by just a few individuals in one or a few plots (e.g., *Cryptopone gilva*, *Pyramica ornata*, *Proceratium pergandei*). The causes of rarity and abundance in ants remain poorly explored. Some authors (e.g., Davidson et al. 2003) have suggested that the most abundant ants (in tropical forest canopies) tend to be homoptera-tenders that can monopolize large territories and pools of sugar resources. In contrast to ants in tropical systems, *A. rudis*, a behaviorally subordinate ant (Fellers 1987, Smallwood 1982), is not known to rely extensively on homoptera exudates, and does not maintain exclusive foraging territories (Lessard, pers. observ.; Smallwood 1982). Instead, *Aphaenogaster rudis*, like other species in the genus *Aphaenogaster* (ants in this genus are referred to as the gypsy ants; T.G. McGlynn, California State University, Dominguez Hills-Carsn, California, pers. comm.), migrates from nest to nest frequently and feeds on a wide variety of food resources. Interestingly, all of these behaviors are shared by *Aphaenogaster araneoides* Emery in Costa Rica, where *A.*

araneoides is extremely abundant in an even more diverse ant community (McGlynn 2006, McGlynn et al. 2004).

The rare ants, those species found at only a few sites, represented a mix of different life histories. Rarity may be real or only apparent. Apparent rarity means that the low abundance of certain species in a set of samples is strictly a sampling artifact. In the current study, the combination of sampling techniques and the high correlation between observed and predicted richness suggest that the species that we describe as being rare actually are rare. Furthermore, species that were rare in space (litter samples) were also rare in time (two years of pitfall trapping), suggesting that they have both low local abundance and low frequency of occurrence at the meso-scale. Most of the rare species may be at the edge of their climate envelope within the GSMNP and hence found predominately at the lowest, warmest, and most diverse sites within the park.

Perhaps not surprisingly, different sampling techniques detected different ant species (Longino et al. 2002, Martelli et al. 2004). The composition of assemblages collected solely by litter extraction did not differ dramatically from the assemblages detected by pitfall traps. However, it is worth noting that there were two *Pyramica* spp. that were detected in the leaf-litter samples that were not collected in the pitfall traps. Similarly the reproductive ant fauna collected in the Malaise traps was different from either the pitfall or leaf-litter samples. Taken together, these results suggest that documenting ant diversity in the GSMNP will require multiple sampling techniques, as is the case in other systems (Delabie et al. 2000, Longino et al. 2002). However, it is worth noting that most (68%) of the identifiable ant species collected here were collected by litter extraction and that the overall patterns of diversity detected by the different methods were highly concordant such that all sampling methods showed similar declines in diversity with increasing elevation.

Conclusions

The ant species that occur at these high-elevation sites generally have broad elevational ranges, whereas many of the species that occur at low elevations are found almost exclusively at low-elevation sites. Similarly, many of the species that occur at high elevations, with broad elevational ranges, also occur at high latitudes (e.g., Lessard and Buddle 2005) and have broad latitudinal ranges. Ant assemblages in GSMNP are highly nested, and most species-poor sites in GSMNP occur at high elevations. This suggests that these broad-ranged species are able to tolerate climatic extremes that are frequent at high elevations and latitudes. Unlike examples of elevational gradients in the southwestern US (e.g., Fleishman et al. 2000), we find few high-elevation endemics and a number of relatively rare species at low elevation. More extensive sampling, especially of other habitat types in GSMNP, could further illuminate the causes and consequences of ant diversity.

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