Rapid Inventory of the Ant Assemblage in a Temperate Hardwood Forest: Species Composition and Assessment of Sampling Methods

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ABSTRACT   Ants are key indicators of ecological change, but few studies have investigated how ant assemblages respond to dramatic changes in vegetation structure in temperate forests. Pests and pathogens are causing widespread loss of dominant canopy tree species; ant species composition and abundance may be very sensitive to such losses. Before the experimental removal of red oak trees to simulate effects of sudden oak death and examine the long-term impact of oak loss at the Black Rock Forest (Cornwall, NY), we carried out a rapid assessment of the ant assemblage in a 10-ha experimental area. We also determined the efficacy in a northern temperate forest of five different collecting methods—pitfall traps, litter samples, tuna fish and cookie baits, and hand collection—routinely used to sample ants in tropical systems. A total of 33 species in 14 genera were collected and identified; the myrmecines, *Aphaenogaster rudis* and *Myrmica punctiventris*, and the formicine *Formica neogagates* were the most common and abundant species encountered. Ninety-four percent (31 of 33) of the species were collected by litter sampling and structured hand sampling together, and we conclude that, in combination, these two methods are sufficient to assess species richness and composition of ant assemblages in northern temperate forests. Using new, unbiased estimators, we project that 38–58 ant species are likely to occur at Black Rock Forest. Loss of oak from these forests may favor *Camponotus* species that nest in decomposing wood and open habitat specialists in the genus *Lasius*.

KEY WORDS   Formicidae, New York, rapid assessment, species richness, structured inventory

Ants and other arthropods are routinely used as indicators of ecological change and ecosystem dynamics (Majer 1983, Andersen 1990, 1997, Kremen et al. 1993, Andersen et al. 2002, Underwood and Fisher 2006). Although ants are ubiquitous, it has proven to be surprisingly difficult either to generate an accurate species list for a particular ecosystem ("strict inventory" of Longino and Colwell 1997) or to estimate patterns of species abundances that allow for precise comparisons among communities ("community characterization" of Longino and Colwell 1997). "Structured inventories" of arthropods incorporate key features of both strict inventories and community characterizations (Oliver and Beattie 1996, Longino and Colwell 1997, Fisher 1999, Bestelmeyer et al. 2000, Longino et al. 2002) and have been applied widely to ant communities (Bestelmeyer and Wiens 2001, Gotelli and Ellison 2002, Ellison et al. 2002, Fisher

2005, King and Porter 2005, Underwood and Fisher 2006).

Forests of the temperate zone, including both deciduous hardwoods and evergreen conifers, account for $\approx 24 \times 10^6$ km², or $\approx 16\%$, of the area of global terrestrial ecosystems; this is about the same as the global area of tropical broad-leaved forest (24.5×10^6 km²) (Whittaker 1975). Like tropical forests, temperate forests are managed heavily for timber, cleared for agriculture, and "converted" for housing; as a consequence, they are increasingly fragmented (Foster et al. 1998, 2003, Kittredge et al. 2003, McDonald et al. 2006). However, in the context of conservation and management, the ant fauna of temperate forests has not been studied nearly as thoroughly as that of tropical forests, deserts, grasslands, or Mediterranean shrublands. In a recent review of 60 studies of survey and monitoring programs of ants (Underwood and Fisher 2006), only 2 studies were conducted in temperate forests; in contrast, 17 were conducted in tropical forests, and the remainder were from a variety of savannas, grasslands, and *Eucalyptus* woodlands.

Unlike most tropical forests, temperate-zone forests are typically dominated by a single tree species or a small number of congeners. Consequently, large-scale outbreaks of pests and pathogens occur more frequently in temperate-zone forests (Wolda 1978, Wallner 1987). These outbreaks can result in the wide-

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spread decline or loss of foundation species that control the distribution and abundance of other species and modulate processes in forested ecosystems (Ellison et al. 2005a). For example, infestation and outbreak of the hemlock woolly adelgid (*Adelges tsugae* Annand) has led to widespread loss of eastern hemlock [*Tsuga canadensis* (L.) Carr.] in southern New England. After the loss of hemlock and a shift in tree species composition toward hardwood stands, there is a shift in ant species composition away from an assemblage dominated by *Aphaenogaster rudis* (Enzmann) s.l. and other myrmicines toward an assemblage dominated by *Formica* spp. and other formicines (Ellison et al. 2005b).

Oaks (*Quercus* spp.) in forests of California and Oregon are currently declining because of infestation by the pathogen *Phytophthora ramorum*, the causal agent of sudden oak death (Rizzo and Garbelotto 2003). Although not yet a problem for eastern oak-dominated forests, *P. ramorum* has been found in nursery stock in southern New England and New York (USDA–APHIS 2004). Several eastern oak species, including the common *Quercus palustris* Muench. (northern pin oak) and *Quercus rubra* L. (northern red oak), have been shown to be highly susceptible to sudden oak death after inoculation with *P. ramorum* (Douglas 2005). Measures to prevent the spread of *P. ramorum* are in place nationwide, and there is significant interest in the impact of oak decline and loss on forest ecosystems. In Cornwall, NY, an experiment has been proposed at the Black Rock Forest to selectively remove all the oak from a large forest block to examine how the loss of this genus will alter long-term dynamics of northern deciduous forests. As part of this study, we were asked to conduct a pretreatment inventory of the ant assemblage in the experimental area and to plan for post-treatment assessments of the effects of the manipulations on the structure and dynamics of the ant assemblages.

The pretreatment inventory presented several challenges. First, although the site is relatively small (10 ha), we had only 4 d to conduct the pretreatment inventory. Second, the ant fauna of New York (or any other northeastern state, except for Ohio; see Coovert 2005) has not been fully documented, so we have no way to quantitatively assess how representative our 4-d sample was, either at a local or a regional scale. Third, standard sampling protocols for ground-foraging and litter-dwelling ants have been developed for tropical forests (Longino and Colwell 1997, Agosti and Alonso 2000, Bestelmeyer et al. 2000, Fisher 2005). The applicability of these methods to forests outside of the tropics has been explored in detail only in Florida (King and Porter 2005), well south of New York.

We used the opportunity to sample the ants at Black Rock Forest to address the following four questions. (1) What is the estimated species richness of ants at this site? We used new, robust asymptotic estimators to extrapolate total species richness from our sample. (2) Do collecting methods and protocols developed for tropical systems work well in a northern temperate forest? In particular, we assessed whether different
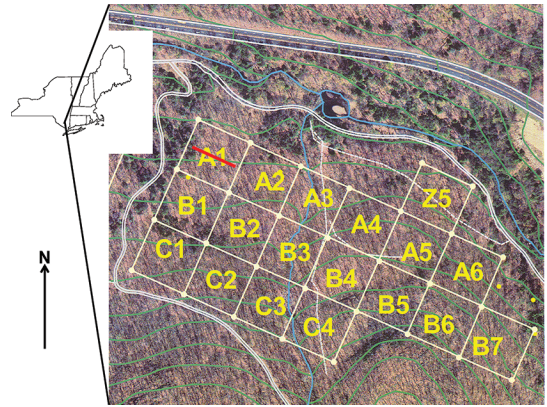

Fig. 1. Map of the 10-ha site of the oak removal experiment, showing the location of Black Rock Forest in New York (inset); the eighteen 75 by 75-m plots; and the placement of one of the sample transects (black line) in one of the plots. A similarly placed transect was sampled in each of the 18 plots.

collecting methods (pitfall traps, litter samples, tuna fish and cookie baits, and visual searching and hand collecting) yielded different sets of ant species and different estimates of local species richness. (3) How is the ant assemblage structured? Using data from samples generally considered to be the least biased (i.e., pitfall traps and litter samples), we examined patterns of relative abundance of the ants in our sample. (4) Can we predict the consequences of loss of oaks for the structure of ant assemblages in the deciduous forests of New York and southern New England? Based on comparisons with existing literature, we attempt some preliminary forecasts.

Materials and Methods

Study Site. We sampled a 10-ha site at the Black Rock Forest (41.45° N, 74.01° W) near Cornwall, NY (Fig. 1). The study site is on the north slope of Black Rock Mountain (400 m a.s.l.). Soils (Chatfield and Rockway series) are derived from glacial till (Denny 1938, Ross 1958). The site was clear-cut in the late 1800s (Tryon 1943) and thinned for cordwood in 1932–1933 and again in 1960 (Harrington and Karnig 1975). This slope is currently covered by a mature ($\approx$120 yr old) oak forest of the "hardwood slope" type of Tryon (1930) or the "red oak association" described by Raup (1938). This forest is dominated by red oak (*Quercus rubra* L.) chestnut oak (*Q. prinus* L.), and black oak (*Q. velutina* Lam.), which account for 33, 21, and 12% of all canopy trees, respectively (W. Schuster, personal communication). Other canopy trees include red maple (*Acer rubrum* L.), sugar maple (*A. saccharum* Marsh.), and black birch (*Betula lenta* L.). Some beech (*Fagus grandifolia* Ehrh.) and black gum (*Nyssa sylvatica* Marsh.) occur in the subcanopy. Based on 1 by 1-m quadrats sampled around each of our ant sampling locations, the most common understory (<1 m tall) species at the site were seedlings and

saplings of the trees *A. rubrum, A. pensylvanicum* L., *Fagus grandifolia, Fraxinus am* L., and *Q. rubra;* the shrubs *Gaylussacia baccata* (Wangenh.) K. Koch., *Hamamelis virginiana* L., and *Kalmia latifolia* L.; the perennial herbs *Aster divericatus* L., *Carex communis* L.H. Bailey, *C. pensylvanica* Lam., *C. swanii* (Fern.) Mackenzie, and *Viola* spp.; and the ferns *Dennstaedtia punctilobula* (Michx.) Moore and *Polystichum acrostichoides* (Michx.) Schott. (All plant nomenclature follows Gleason and Cronquist 1991.)

Ant Sampling. Ants at the 10-ha site were sampled 6–9 July 2006 using pitfall traps, sieved litter, and hand collections (a modified version of the ALL protocol of Agosti and Alonso 2000), as well as two types of baits, oil-packed tuna (Bumble Bee Chunk Light; Bumble Bee Foods, LLC, Toronto, ON, Canada) and cookies (Pecan Sandies; Kellogg Co., Battle Creek, MI) (Bestelmeyer et al. 2000). A 75-m-long transect oriented in a southeasterly direction was established through the center of each of eighteen 75 by 75-m plots (Fig. 1). Along each transect, we sampled 10 points located every 6.5 m along the transect beginning 6.5 m from the plot edge. Thus, we sampled 10 points/transect × 1 transect/plot × 18 plots = 180 sample points in the 10-ha forest block. At each sample point, we placed a pitfall trap consisting of a 95-mm-diameter plastic cup buried flush with the substrate surface. Traps were filled with 20-ml soapy water and left to accumulate ants for 48 h. Trap contents were collected and fixed in the field in 95% EtOH. After collection of the pitfall traps, two baits were set up at each sample point. Equal volumes (≈1 cm^3) of either tuna or cookie were set out in 55-mm-long by 15-mm-diameter white, plastic vials. Baits were set out during the middle of the day for 1 h, after which time vials with accumulated ants were collected, filled with 95% EtOH, and capped. Litter-dwelling ants were extracted from three 1-liter leaf litter samples per transect. Litter was chopped and sieved in the field, and all ants extracted from the litter were aspirated into 95% EtOH. Last, we searched for and hand-collected ants for one person-hour throughout each plot, looking under rocks, on low-growing vegetation, and in the leaf litter. When a nest was encountered, a minimum of five individuals was collected, along with males and queens when possible. Not more than 2 min was spent collecting from a single nest. No rain fell during the 4-d sample period. Ants were sorted and identified by the authors; identifications were confirmed by Stefan Cover (Harvard University Museum of Comparative Zoology [MCZ]). Vouchers are deposited at the MCZ. Nomenclature follows Bolton et al. 2006.

Data Analysis. We estimated the species richness of the site based on data from each collecting method and compared quantitatively the relative sampling efficiencies of pitfall traps, tuna baits, cookie baits, litter samples, and hand collecting, all of which were used in the 18 plots. The data for such an analysis consist of replicated collections of individuals that have been sorted to species and counted. The raw data can be downloaded from the

Harvard Forest Data Catalog (http://harvardforest.fas.harvard.edu/data/archive.html), dataset HF-097.

We used three different statistical methods to estimate species richness and compare among the five sampling methods: (1) asymptotic richness estimators, which provide a conservative (minimum) estimate of the number of species that are present, but were not collected in the samples (Colwell and Coddington 1994); (2) rarefaction, which standardizes species richness across sampling methods on the basis of a common number of samples or incidences; (3) similarity analyses, which compare the species composition of two sampling methods by estimating the number of shared species (Chao et al. 2005).

Even with standardized sampling, it is challenging to compare biodiversity measures because the results are sensitive both to the number of individuals and to the number of samples collected (Gotelli and Colwell 2001). Studies of ant biodiversity represent a special challenge because the natural "units" of biodiversity are the number of distinct colonies, but the data consist of samples of individual workers. For example, if a pitfall trap captures 20 workers of *Formica fusca*, the true number of independent colonies sampled is between 1 and 20 and is probably much closer to 1. However, 20 workers collected from hand-sampling at different nests probably represent closer to 20 independent colonies, because those workers may have been taken from nests that were many meters apart from one another. For this reason, we initially conducted two rarefaction analyses, one using abundance data and the other using incidence data. We found that the results of both analyses were qualitatively similar, so we report here only the more conservative method, which is to count incidences, not abundances (Longino and Colwell 1997).

Asymptotic Estimates of Species Richness. To estimate asymptotic species richness of the 10-ha site, we used the Chao1 index (Chao 1984) as calculated by EstimateS version 7.5.1 (Colwell 2005):

$$S_{Chao1} = S_{Obs} + \frac{F_1^2}{2F_2} \qquad [1]$$

where S_{Obs} is the total number of species observed, F_1 is the number of species represented by exactly one incidence in the collection (uniques), and F_2 is the number of species represented by exactly two incidences in the collection (duplicates). We also plotted 95% asymmetric confidence intervals (CIs) associated with these estimates of species richness (Colwell 2005). For the analysis of asymptotic estimators, we pooled the data for all the replicate traps within each collection type.

Rarefaction Analyses. Rarefaction methods yield the expected number of species based on a random subsample of the data and enable one to rank the different collecting methods according to the expected number of species that would be found for a standardized sampling effort. Following the protocol in Gotelli and Colwell (2001), we first generated sample-based rarefaction curves for each collection

method. In sample-based rarefaction, the different samples within a collection method are randomly combined to generate a species accumulation curve. We conducted two sets of sample-based rarefaction analyses, one using the individual trap as a sampling unit, and one using the individual plot as a sampling unit. First, for the trap-level analyses, we considered the total set of traps in the 10-ha sampling area without reference to the particular plot in which they occurred. In this trap-level analysis, we had different sample sizes for each sampling method: 180 each of pitfall traps, tuna baits, and cookie baits; 54 litter samples, and 18 hand collections. Second, for the plot-level analyses, we aggregated the traps for each sampling method (10 pitfalls, 10 tuna baits, 10 cookie baits, or 3 litter traps) within a plot, so for this analysis we had equal sample sizes ($N = 18$) for each sampling method.

Next, these sample-based rarefaction curves were rescaled to a common x-axis of incidence (Gotelli and Colwell 2001). This rescaling is necessary and important because the collection methods differed greatly in the number of individuals and incidences they accumulated. For example, the average hand collection yielded 82 individuals, 13 species incidences, and 9 species, whereas the average pitfall sample yielded only 2 individuals, 1 species incidence, and 1 species. Without adjusting for these sampling differences, a single hand collection would always be expected to yield more individuals and incidences—and therefore more species—than a single pitfall trap.

We used new analytical methods (Colwell et al. 2004) that treat the total collection as a sample of a larger statistical universe (the entire assemblage) to generate statistically robust and valid CIs for the rarefaction curves. These CIs do not converge to zero at the maximum sample size, unlike CIs constructed with previously published methods. Calculations and simulations were done with EstimateS, version 7.5.1 (Colwell 2005).

Similarity Among Collection Methods. Comparisons of rarefaction curves and asymptotic estimators allowed us to evaluate differences among the sampling methods in species richness and relative abundance distributions (which in turn affect the shape of the rarefaction curve). However, two collection methods might yield the same rarefaction curves and asymptotic estimators, yet have no species in common. For example, in some ant communities, there is a distinctive litter fauna (dominated by the subfamily Ponerinae) that may be poorly sampled by traps or pitfalls. Conversely, species composition at baits may be biased toward over-representation of behaviorally dominant species. Thus, it is important to also estimate the compositional similarity of collections that are based on different sampling methods.

To evaluate similarity, one could calculate the classic Jaccard similarity index J_{ij} (Jaccard 1901) between each pair of collection methods:

$$J_{ij} = \frac{c}{a + b + c} \qquad [2]$$

where a is the number of species unique to sample i, b is the number of species unique to sample j, and c is the number of species common to both samples. J_{ij} ranges from 0 to 1; a value of 0 indicates no shared species between samples, whereas a value of one indicates that all species are shared between the two samples. Unfortunately, this index is inherently biased toward small values of J_{ij} because it does not take into account (rare) shared species that were not represented in either of the two sample collections. To adjust for this bias, we used an abundance-based Jaccard Index developed by Chao et al. (2005):

$$\hat{J}_{abd} = \frac{\hat{U}\hat{V}}{\hat{U} + \hat{V} - \hat{U}\hat{V}}, \qquad [3]$$

where

$$\hat{U} = \sum_{j=1}^{D_{12}} \frac{X_i}{n} + \frac{(m-1)}{m} \frac{f_{+1}}{2f_{+2}} \sum_{i=1}^{D_{12}} \frac{X_i}{n} I(Y_i = 1) \qquad [4]$$

and

$$\hat{V} = \sum_{i=1}^{D_{12}} \frac{Y_i}{m} + \frac{(n-1)}{n} \frac{f_{1+}}{2f_{2+}} \sum_{i=1}^{D_{12}} \frac{X_i}{m} I(X_i = 1). \qquad [5]$$

The additional terms in equations 4 and 5 are as follows. For two assemblages (e.g., incidence records from two of our trapping methods) to be compared, we sample at random n individuals from assemblage 1 and m individuals from assemblage 2. We write the frequencies of each species in sample 1 (from assemblage 1) as $(X_1, X_2,.., X_{S1})$ and the frequencies of each species in sample 2 (from assemblage 2) as $(Y_1, Y_2,.., Y_{S2})$. If species i is missing from either sample, X_i or $Y_i = 0$. If a species is truly shared by the two assemblages, (X_i, Y_i) denotes the pair of frequencies of a single shared species. The value S_{12} is the total number of species that the two assemblages have in common, and the value D_{12} is the number of species shared by the two assemblages that are actually observed in the two samples. Thus, $D_{12} \le S_{12}$, and the difference $S_{12} - D_{12}$ is the number of shared species that are absent from one or both of the samples. The indicator function $I(X_i = 1)$ means $I = 1$ if $X_i = 1$ and $I = 0$ otherwise. Last, f_{1+} is the observed number of shared species that are uniques ($X_i = 1$) in sample 1 and f_{2+} is the observed number of shared species that are duplicates ($X_i = 2$) in sample 1. Similarly, f_{+1} and f_{+2} are the observed number of shared species that are uniques and duplicates in sample 2 ($Y_i = 1$ and $Y_i = 2$, respectively). To avoid division by 0, if either f_{2+} or $f_{+2} = 0$, they are set equal to 1 in equation 4 or 5. We used 1,000 random bootstrap samples to calculate 95% CIs for this index. If the CIs encompass 1.0, we cannot reject the null hypothesis that the two collection methods share the number of species that would be expected on the basis of chance. Calculation of $\hat{J}_{abd}$ and construction of bootstrapped CIs were done using EstimateS version 7.5.1 (Colwell 2005). As with the rarefaction analyses described above, we used incidences as our measure of abundance of ants in our calculations of $\hat{J}_{abd}$.

Table 1. Species collected in the 10-ha oak stand at Black Rock Forest

	Pitfall	Litter	Tuna	Cookies	Hand
Ponerinae					
Amblyopone pallipes (Haldeman)	√				√
Dolichoderinae					
Tapinoma sessile (Say)		√			√
Formicinae					
Acanthomyops claviger (Roger)					√
Acanthomyops interjectus (Mayr)					√
Acanthomyops latipes (Walsh)					√
Acanthomyops murphyi (Forel)					√
Brachymyrmex depilis Emery	√				√
Camponotus chromaiodes Bolton	√				√
Camponotus noveboracensis (Fitch)					√
Camponotus pennsylvanicus (De Geer)	√		√	√	√
Formica aserva Forel					√
Formica integra Nylander					√
Formica lasiodes Emery		√			
Formica neogagates Viereck	√	√	√	√	√
Formica nitidiventris Emery					√
Formica podzolica Francoeur	√		√		√
Formica subaenescens Emery	√		√		√
Formica subsericea Say	√				√
Lasius alienus (Foerster)	√	√			√
Lasius nearcticus Wheeler					√
Lasius speculiventris Emery					√
Lasius umbratus (Nylander)	√		√		√
Prenolepis imparis (Say)	√	√			√
Myrmecinae					
Aphaenogaster rudis (Enzmann)	√	√	√	√	√
Myrmecina americana Emery		√			
Myrmica punctiventris Roger	√	√	√	√	√
Myrmica sculptilis (*sensu* Francoeur)	√				√
Myrmica smithana (*sensu* Francoeur)				√	
Protomognathus americanus (Emery)					√
Stenamma impar Forel	√	√			√
Stenamma schmitti Wheeler	√				
Temnothorax curvispinosus (Mayr)		√			
Temnothorax longispinosus (Roger)	√	√	√	√	√
Total species collected	17	11	8	6	28

A √ indicates presence in each of the trap types or in the set of ants collected during searches.

Assemblage Composition and Relative Abundance. Rank-abundance diagrams were constructed for the litter and pitfall samples (which give the least unbiased counts of individual workers). We tested for differences in species rank abundances between the two samples using the Kolmogorov-Smirnov goodness-of-fit test (Gotelli and Ellison 2004) implemented in S-Plus version 7.0 (Insightful, Seattle, WA).

Results

Estimates of Species Richness. We collected 3,133 individual ants from the four ant subfamilies (Ponerinae, Dolichoderinae, Formicinae, and Myrmicinae) that are known to occur in New York. These individuals represent 689 occurrences (incidences) in pitfall traps, at baits, in litter samples, and in hand collections. From these individuals, we identified 33 species in 14 genera (Table 1). These species include soil-, litter-, and ground-dwelling species, wood and litter decomposers, and slave-makers. The estimated total species richness at the site depended on collection method, and ranged from seven species based on cookie baits to 31 species based on hand collections (Fig. 2). Estimated species richness was 22 species based on pitfall traps and 21 species based on sieved litter samples. Because of the large number of uniques and duplicates in the sieved litter samples, the 95% CI on this point estimate ranged from 12 to 63, much broader than for any other collection method (Fig. 2).

We estimated total species richness of the entire site by pooling all incidences across all trap types in each of the 18 plots—analogous to considering our total
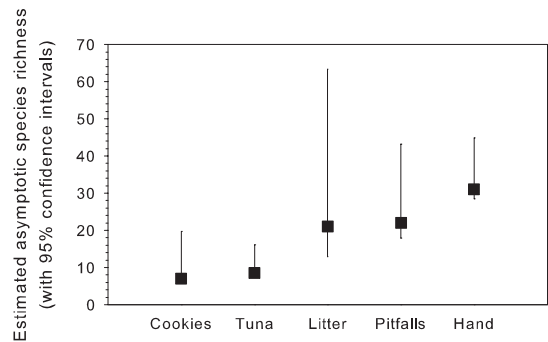

Fig. 2. Asymptotic estimates of species richness at the 10-ha experimental site based on the five collection methods.

Fig. 4. Plot-level rarefaction curves for the five collection methods, corrected for the number of incidences in the samples. For clarity, the 95% CIs (gray areas) are shown only for the hand collection during visual searches. Widths of CIs are similar for the four other collection methods.
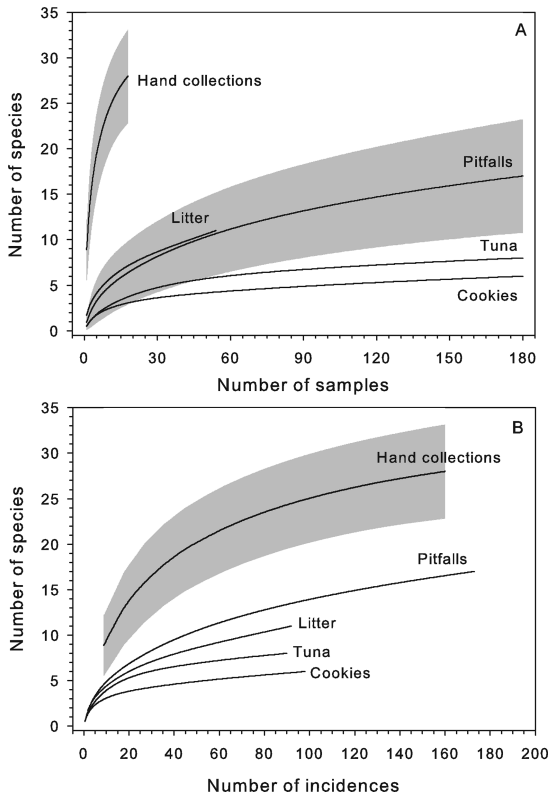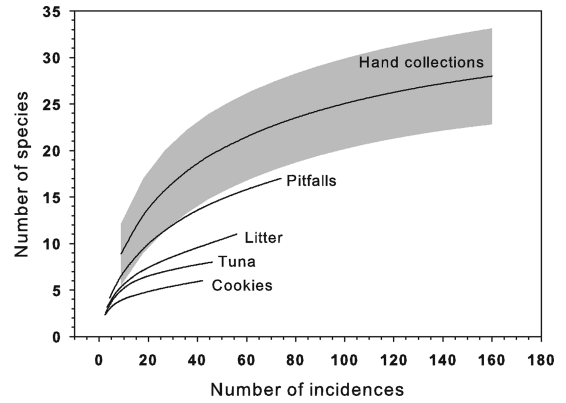

Fig. 3. Trap-level rarefaction curves for the five collection methods. (A) Rarefaction curves based on the number of samples. For clarity, the 95% CIs (gray areas) are shown only for the hand collection during visual searches and the pitfall traps. Widths of CIs are similar for the three other collection methods. (B) Rarefaction curves corrected for incidences. For clarity, the 95% CIs (gray areas) are shown only for the hand collection during visual searches. Widths of CIs are similar for the four other collection methods.

collection of 3,133 ants as having come from one sample, and computing the Chao1 estimator S_{Chao1} for this aggregate "sample." The estimated total species richness for the site is 38 species. Because six species (the formicines *Camponotus noveboracensis* and *Lasius speculiventris*, and the myrmecines *Myrmecina americana*, *Myrmica smithana*, *Stenamma schmitti*, and *Temnothorax curvispinosus*) are each represented by only one individual in our collection, the 95% CI on this point estimate is quite large: 34.3–57.7.

Differences Among Collecting Methods. Hand collection always yielded ants in every plot (minimum = 46 individuals per plot, maximum = 126 individuals per plot). Not all of the samples from the other collecting methods accumulated ants: 99/180 pitfall traps (55%), 87/180 tuna baits (48%), 93/180 cookie baits (52%), and 50/54 (93%) of litter samples had at least one ant. There were no correlations among methods in the number of traps or baits accumulating ants along each transect within each of the 18 plots ($r = 0.36, 0.07,$ and 0.17 and $P = 0.15, 0.80,$ and 0.49 for pitfall versus tuna

baits, pitfall versus cookie baits, and tuna versus cookie baits, respectively).

Rarefaction analyses of trap-level data (i.e., rarefaction of individual samples without reference to the plot in which each sample was located) revealed that hand collection during visual searches resulted in significantly more species, whether or not the analyses were performed on samples or corrected for number of incidences (Fig. 3). Rarefaction curves for pitfall trap and litter collections on a sample basis were nearly identical (Fig. 3A), whereas pitfall traps accumulated species a bit more rapidly (but not significantly more rapidly, as determined by overlap of 95% CIs) when the rarefaction curves were corrected for incidences (Fig. 3B). On both a sample basis and on an incidence basis, rarefaction curves for tuna baits and cookie baits were not significantly different from each other (Fig. 3). The pitfalls and litter samples accumulated species significantly more rapidly than did the baits, either on a per-sample basis (Fig. 3A) or when corrected for numbers of incidences in the samples (Fig. 3B).

Identical patterns were found when the data were analyzed at the plot level (Fig. 4). Hand collection during visual searches always accumulated species more rapidly than pitfall or litter samples, which in turn accumulated species more rapidly than tuna or cookie baits.

Similarity in Species Composition Among Collecting Methods. The five different collection methods generally obtained similar species. Adjusted compositional similarity (from equation 3) was close to one (100%) in all pairwise comparisons except for comparisons of cookie baits versus hand sampling during visual searches (Fig. 5). The 95% CIs on all pairwise adjusted similarities included 1.0.

Uniques occurred in each collection method except for tuna baits. In pitfall traps, *Brachymyrmex depilis*, *F. subaenescens*, *C. chromaiodes*, *A. pallipes*, and *Stenamma schmitti* were each represented by a
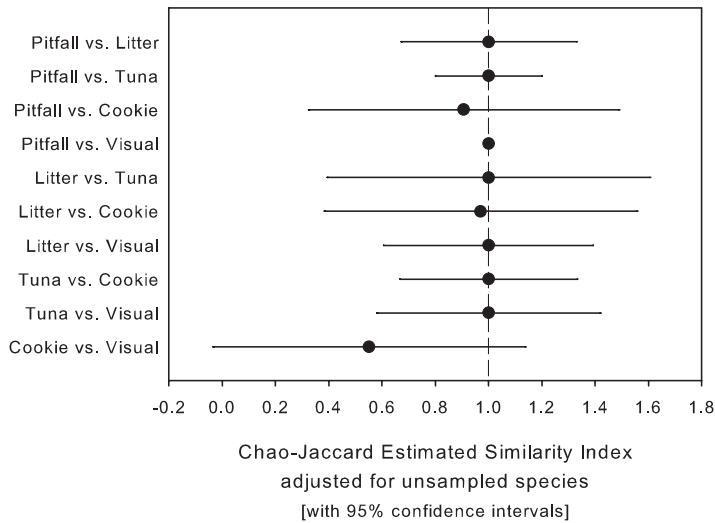
Fig. 5. Similarity in species composition among the five collection methods, adjusted for unsampled species (equation 3, with 95% CIs).

single individual. In litter samples, *Tapinoma sessile*, *Myrmecina americana*, and *Temnothorax curvispinosus* were uniques. At cookie baits, *C. pennsylvanicus* and *Myrmica smithana* were uniques. In hand collections, *Stenamma impar*, *Camponotus noveboracensis*, and *Lasius speculiventris* were all uniques. Of these 13 collection method–specific uniques, all but 1 (*S. schmitti*) of the pitfall uniques also were collected in the hand samples (as well as in some of the other methods), as was *T. sessile* (a litter-sample unique) and *C. pennsylvanicus* (a cookie-bait unique).

Structure of the Black Rock Ant Assemblage. A single species, *Aphaenogaster rudis*, accounted for 57% of all individuals collected and was the most frequent species collected by all of the methods (38, 53, 81, 89, and 43% in pitfall traps, litter samples, at tuna baits, at cookie baits, and in hand collections, respectively). In both pitfall traps and litter samples, the other dominant species were *Formica neogagates* and *Myrmica punctiventris.* At the other extreme, five species were represented by only a single specimen in pitfall traps and three others were unique to litter samples. The rank abundances of species did not differ (Kolmogorov-Smirnov test statistic = 0.286, P = 0.365) between our samples collected using pitfall traps and litter samples (Fig. 6).

Discussion

Our 4-d inventory of the ants of Black Rock Forest allowed us to estimate overall ant species richness, provided an assessment of the use of different collecting methods in a north-temperate forest, and showed clear patterns of commonness and rarity in the local ant fauna. This inventory also set the baseline for future assessments of the impact of the loss of red oak on the ant fauna.

Ant Diversity at Black Rock Forest. Based on the results of all of the sampling methods combined, we estimate that the 10-ha experimental area at Black Rock Forest is home to 38 species of ants. Because there is no comprehensive list of the ants of New York, of any bordering state (except Ohio), or of any bordering Canadian Province, it is impossible to know how representative of the local or regional ant fauna is our collection of ants from Black Rock. Forty years ago, Wilcox (1965) suggested that New York has ≈90 species of ants, but provided no list. Coovert (2005) reported 118 ant species from Ohio, but 26 of these occur only in the southern part of the state that was never glaciated and are unlikely to occur in formerly glaciated New York State. Stefan Cover has collected nearly 100 species from Massachusetts (personal communication), but many of these are specialists in unique habitat types, including sand plains, open grasslands, pitch-pine barrens, and bogs (see also Gotelli and Ellison 2002, Ellison et al. 2002) that do not occur in the Hudson Highlands of New York. In our rapid inventory at Black Rock Forest, we collected 33 species that were either abundant or uncommon and that represented a wide range of ecological groups, including soil-, litter-, and ground-nesting species, omnivores and decomposers, nest parasites, and slave-makers. Thus, we are confident that our sampling was unbiased with respect to habitat or ant lifestyle and is broadly representative of the local ant fauna.

The 95% CI on our estimate of species richness at Black Rock extends to nearly 58 species, and further collection undoubtedly would yield additional species. Based on other taxonomic and ecological studies in the New York–New England region, Ohio distribution records (Coovert 2005), and S. Cover's preliminary list of the ants of Massachusetts, there are at least 12 additional species we would expect to find in the relatively dry deciduous oak forests at Black Rock. These include five relatively small and cryptic myrmicines, *Stenamma brevicorne* (Mayr), *S. diecki* Em-
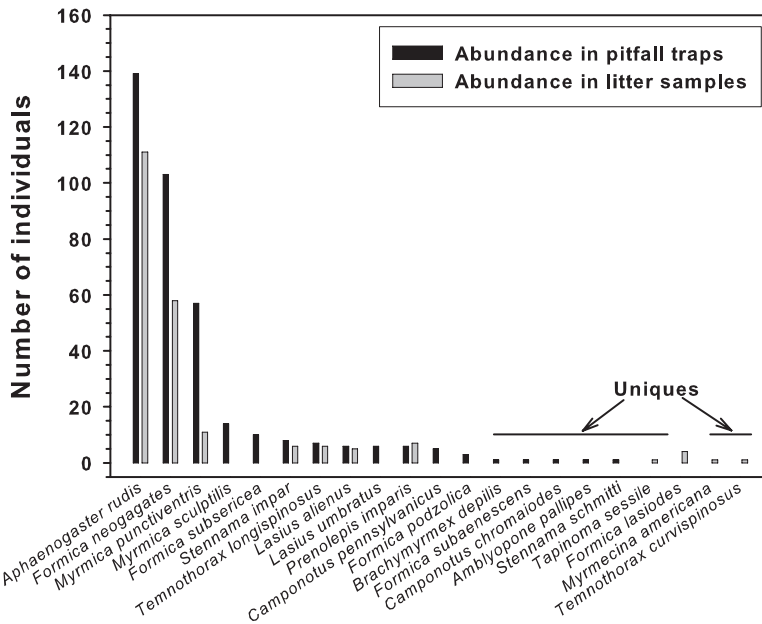
Fig. 6. Abundance of ant species from pitfall traps and litter samples. The species are ordered by their abundance in pitfall traps.

ery, *Solenopsis molesta* (Say), *Temnothorax ambiguus* (Emery), and *T. schaumii* (Roger); several similarly cryptic ponerines, *Hypoponera punctatissima* (Roger), *Ponera pennsylvanica* Buckley, and several species of *Proceratium;* two larger myrmicines, *Crematogaster cerasi* (Fitch) and *C. lineolata* (Say); and three large formicines, *Formica obscuriventris* Mayr, *F. neorufibarbis* Emery, and *Acanthomyops subglaber* (Emery).

Efficacy of Different Collecting Methods. Our results clearly indicate that hand sampling accumulates species more rapidly and in greater number than pitfall trapping, litter sieving, or baiting (Figs. 2–4). Moreover, there were no significant differences in composition of species accumulated by the different collecting methods (Fig. 5). Only a few additional rare species were collected in litter samples, baits, or pitfall traps that were not collected by hand sampling. This result is not surprising, because there are not large numbers of ants that nest only in the leaf litter or in the tree canopy of north temperate forests, in contrast to tropical forests. Because we conducted hand sampling in a fixed time interval (one person-hour) and limited the amount of time spent collecting at a given nest, this method can provide a quantitative measure of ant species richness in northern forests and probably in many other habitats (e.g., grasslands, deserts) that do not support a substantial arboreal or litter-ant fauna. Sorting through pitfall traps and litter samples is extremely time- and labor-intensive (King and Porter 2005) and may not be worth the effort in northern temperate forests when the goal is the rapid assessment of species number and relative abundance. However, where there are many cryptic species that are restricted to habitats that are hard to search or sample

by hand, the advantage of hand sampling is diminished relative to other sampling methods.

We note that the efficiency of collecting ants by hand sampling can be affected by the expertise of the collector. Experienced collectors can locate nests more rapidly. However, they may focus their attention on collecting uncommon, rare, or "interesting" species while ignoring the more common, "less interesting" ones. In contrast, less experienced collectors may take more time to find nests but are more likely to collect from every nest, even when the species is abundant. Accurate assessments of diversity and abundance require unselective collections made from as large a number of nests as possible, so striking a balance between experience and sampling bias is critical.

Both cookie and tuna baits performed poorly, supporting prior studies that found that baits tend to accumulate a small number of behaviorally dominant or abundant species. Setting out and recovering grids of pitfall traps or baits and extracting litter samples with Berlese funnels or Winkler sacks is time-consuming and labor-intensive, and these methods may not even be feasible in many habitats with rocky soil or negligible leaf litter. We conclude that structured hand sampling is sufficient to assess species richness and composition of ant assemblages in north-temperate forests.

Structure of the Black Rock Ant Assemblage. Three species—*A. rudis*, *F. neogagates*, and *M. punctiventris*—numerically dominated the ant fauna of the oak forests at Black Rock (Fig. 6). These are all ecological generalists and occur in a broad range of habitats throughout the northeastern United States (Herbers 1989, Banschbach and Herbers 1999, Gotelli and Ellison

2002, Coovert 2005, Backus et al. 2006). Further sampling and accumulation of additional species is not likely to alter our assessment of the dominant species in this system. None of the species that we would expect to encounter with additional intensive sampling occurs either in large nests or in large numbers, and it is unlikely that we would collect them in sufficient numbers to alter the shape of the relative-abundance curve for this site (Fig. 6). To determine the response of this ant assemblage to large-scale vegetation change, future research should examine the functional role of these three numerically dominant species in northern forests, rather than focusing on more intensive collecting of rare species that would fill out the relative-abundance curve.

Future of the Ant Assemblages at Black Rock Forest. Because the Black Rock Forest has not been disturbed by significant logging or land use changes in nearly a century (Tryon 1943, Harrington and Karnig 1975), the ant assemblage is likely to be at as close to an equilibrium state as one could expect to find in a northern forest outside of an old-growth stand. What would happen to this assemblage if oaks were removed, either by selective logging or by sudden oak death? Because oak makes up >60% of the canopy at Black Rock, its loss would create more open habitat that might favor *Lasius neoniger*, *L. speculiventris*, and *L. flavus* over the woodland *Lasius* species currently abundant at the site. Standing dead timber could provide additional food and habitat for *Camponotus* spp., increasing their abundance. *Temnothorax* spp. might decline in abundance as the acorns in which they nest disappear. However, this species also nests in hollow twigs and other small cavities. Logging slash and abundant twigs from dying trees could make up for the lost acorns, providing more than enough new nesting sites for *Temnothorax.*

Early successional forests in New York and New England are dominated by fast growing hardwoods, including birch (*Betula* spp.) and red maple (*Acer rubrum* L.). Ant species composition of such young deciduous forests is similar to that found in oak forests (Ellison et al. 2005b), although *Formica* and *Camponotus* spp. tend to be numerically more abundant than *A. rudis.* Climate change and subsequent northward range shifts of southern species (Folgarait 1998, Parmesan 2006, Snyder and Evans 2006) are more likely to have substantial qualitative and quantitative impacts on the ant fauna at Black Rock Forest. The results presented here will allow us to determine if and when such changes occur.

Acknowledgments

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