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Research

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Effectiveness of Winkler Litter Extraction and Pitfall Traps in Sampling Ant Communities and Functional Groups in a Temperate Forest

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Abstract

Selection of proper sampling methods for measuring a community of interest is essential whether the study goals are to conduct a species inventory, environmental monitoring, or a manipulative experiment. Insect diversity studies often employ multiple collection methods at the expense of researcher time and funding. Ants (Formicidae) are widely used in environmental monitoring owing to their sensitivity to ecosystem changes. When sampling ant communities, two passive techniques are recommended in combination: pitfall traps and Winkler litter extraction. These recommendations are often based on studies from highly diverse tropical regions or when a species inventory is the goal. Studies in temperate regions often focus on measuring consistent community response along gradients of disturbance or among management regimes; therefore, multiple sampling methods may be unnecessary. We compared the effectiveness of pitfalls and Winkler litter extraction in an eastern temperate forest for measuring ant species richness, composition, and occurrence of ant functional groups in response to experimental manipulations of two key forest ecosystem drivers, white-tailed deer and an invasive shrub (Amur honeysuckle). We found no significant effect of sampling method on the outcome of the ecological experiment; however, we found differences between the two sampling methods in the resulting ant species richness and functional group occurrence. Litter samples approximated the overall combined species richness and composition, but pitfalls were better at sampling large-bodied (*Camponotus*) species. We conclude that employing both methods is essential only for species inventories or monitoring ants in the Cold-climate Specialists functional group.

Key words: Formicidae, sampling method, functional group, Amur honeysuckle, white-tailed deer

Within the past few decades, several insect taxa, such as ants, beetles, and pollinators, have emerged as potentially valuable environmental indicators that are sensitive to disturbance, land use, or management in terrestrial ecosystems (Kevan 1999, Andersen and Majer 2004, Koivula 2011). Insects are advantageous for environmental monitoring because they are highly diverse, even in small areas; inexpensive to collect in large numbers; may be well represented in historical or reference collections; and are sensitive to a wide range of disturbances (Kremen et al. 1993). The disadvantages are that many insect taxa may require multiple complementary sampling methods and it may be time-consuming and expensive to process and identify large numbers of specimens (Longino et al. 2002).

Ants are becoming widely used in environmental monitoring and ecological experiments because they are highly abundant in most terrestrial ecosystems and taxonomic keys for species-level identification are available for several regions and at the global scale for any genera (Underwood and Fisher 2006). Ant species diversity and composition may change in predictable ways along environmental gradients or during recovery following ecosystem disturbance, and the responses of ants may be highly correlated with those of other taxa (Andersen and Majer 2004, Underwood and Fisher 2006). For example, ant species richness in grasslands increases in years following restoration (Campbell and Crist 2017), and increased ant richness was mirrored by ant indicator metrics that were associated with other insect taxa and birds (Peters et al. 2016).

Ant functional groups (*sensu* Andersen 1995) are often used as environmental indicators partly because of their success in monitoring restoration and recovery from mining or grazing practices in Australia (Andersen and Majer 2004). These functional groups, based on behavioral dominance and genus-level classifications, have been modified and applied to semiarid regions in North and South America (Bestelmeyer and Wiens 1996, Andersen 1997), tropical rainforests of Central and South America (Gómez et al. 2003), and to a lesser extent, the grasslands of North America

(Jurzenski et al. 2012, Moranz et al. 2013). In these applications, ant functional groups respond differently to disturbance and land use. For example, recovery of mine sites following restoration is indicated by decreases in the Dominant Dolichoderinae and Opportunists functional groups and increases in Cryptic Species (Ottonetti et al. 2006). Ant functional groups have not been applied to northern temperate forests until recently. Ellison (2012) modified the functional groups to include ants of eastern North America, and provided support for the use of ants as indictors in temperate forests.

The use of ant species diversity or functional group structure to answer ecological questions hinges on consistent and informative sampling techniques. Most ant studies employ passive sampling techniques (i.e., pitfall traps or litter extractions using Winkler bags or Berlese funnels) that are easily replicated among researchers (Bestelmeyer et al. 2000). Passive sampling methods rely on either ant surface activity (pitfall traps) or on the detection of ants that are present in litter samples at a specific time. Therefore, passive methods may not detect ants of all body sizes in all habitat types (Olson 1991, Bestelmeyer et al. 2000). Pitfall traps are more effective at capturing actively moving ants in open habitats with shallow litter layers (Parr and Chown 2001, Souza et al. 2012, Wiezik et al. 2015), thereby overrepresenting large active ants compared with small, sedentary species (Olson 1991). In contrast, litter sampling is more effective in habitats with deeper litter layers (Fisher 1999, Groc et al. 2007, Ivanov and Keiper 2009) and tends to capture resource specialist species (Olson 1991). Litter samples can also be expressed as absolute densities of species richness and abundance per unit area (Bestelmeyer et al. 2000). However, litter samples represent a snapshot in time, while pitfall traps are in the field continuously over days, collecting ant species with a wider range of thermal and temporal niches. Therefore, use of both pitfalls traps and litter collection techniques should provide complementary information on the ant community.

Sampling methods are also dependent on the goal of the study. For biodiversity inventories, a combination of methods is encouraged to sample the widest range of ant species (Bestelmeyer et al. 2000). To create a standardized protocol for collection of ground-dwelling ants, Agosti and Alonso (2000) developed the Ants of the Leaf Litter (ALL) Protocol. The ALL Protocol utilizes pitfalls and Winklers in combination and has been extensively used in tropical regions with high species diversity and turnover in species composition (Olson 1991, Fisher et al. 2000, Longino et al. 2002; but see Souza et al. 2012). However, ant species diversity and turnover in composition is lower in temperate than tropical regions (Dunn et al. 2007). Therefore, the use of only one of these methods may be adequate to sample temperate ants, a potential advantage for researcher time and expenses.

Many studies have tested the relative efficacy of different collection techniques and their combinations for characterizing total ant species richness or composition; however, few temperate studies have compared methods for addressing ecological questions. Wiezik et al. (2015) found that pitfall samples in two different habitats and in the intervening ecotone yielded significant differences in ant species richness across habitats, but not from Winkler litter extractions. Other studies have tested effects of collection methods on ant species richness and composition found in different habitats (Martelli et al. 2004, General and Thompson 2008, Tista and Fiedler 2011), but we are unaware of studies comparing sampling methods that measure ant community responses to a controlled experimental design.

Two important drivers of ecosystem change in forests of the eastern United States are the overabundance of white-tailed deer (*Odocoileus virginianus* (Zimmermann)) and the widespread occurrence of invasive plants, such as the understory shrub, Amur honeysuckle (*Lonicera maackii* (Ruprecht); Côté et al. 2004, McNeish and McEwan 2016). Preferential browsing by white-tailed deer and invasion of Amur honeysuckle reduce native plant abundance and richness, increase invasive plant success, change forest structure, and homogenize the plant community (Gould and Gorchov 2000, Rooney 2008, Knight et al. 2009, McNeish and McEwan 2016). Deer and honeysuckle also alter leaf litter decomposition, soil nutrients, and microclimates (McKinney and Goodell 2010, Bressette et al. 2012, Shelton et al. 2014). Therefore, both of these drivers of change may have bottom-up effects on ground-dwelling arthropods. Ground-dwelling arthropods have a range of responses to the presence of these species, including reduced abundance of spiders (Buddle et al. 2004, Bressette et al. 2012, Christopher and Cameron 2012), ants (Lessard et al. 2012), and other arthropods (Bressette et al. 2012, Christopher and Cameron 2012).

We assessed the effectiveness of pitfall and litter samples for measuring the species richness and functional group composition of ground-dwelling ants in response to experimental removals of white-tailed deer and Amur honeysuckle in an eastern temperate forest. Our study had three objectives: 1) identify any differences in overall ant species richness and composition between pitfall samples and Winkler litter extractions; 2) determine whether the structure of any functional groups differed between the two sampling methods; and, 3) evaluate whether pitfall or litter sampling led to similar conclusions from hypothesis tests on the main or interactive effects of deer and honeysuckle removal. This study represents the first to compare these techniques for characterizing ant diversity and functional groups composition in response to experimental removal of a keystone herbivore and an invasive shrub in temperate forest ecosystems.

Materials and Methods

Study Sites

The study was conducted in southwestern Ohio within mid-successional deciduous forests. Five study sites—Bachelor Preserve, College Woods, Kramer Woods, Reinhart Preserve, and Western Woods—were located within Miami University's Natural Areas (a preserve of >400 ha) near Oxford, OH. The climate of the area is temperate continental, characterized by cold winters, hot summers, moist springs, and dry autumns. The study sites are located on similar upland topographic positions (253 ± 5 m.a.s.l.), and the dominant soil type at the sites is fine, mixed active Hapludalfs. Average distance between sites is 2.15 ± 0.34 km; the minimum distance between sites is 0.90 km and the maximum is 3.86 km. Average distance from each site to a forest edge is 152 ± 24 m; the minimum distance to a forest edge is 67 m. Dominant hardwood species at these sites include sugar maple (*Acer saccharum* Marshall), elm (*Ulmus* spp.), oak (*Quercus* spp.), hickory (*Carya* spp.), and American beech (*Fagus grandifolia* (Ehrhardt)). The invasive Amur honeysuckle (*L. maackii*) dominated the understory of these sites, with 30–50% canopy cover. Common herbaceous species included common black snakeroot (*Sanicula odorata* Pryer & Phillippe), false nettle (*Boehmeria cylindrical* (L.)), Virginia creeper (*Parthenocissus quinquefolia* (L.)), and garlic mustard (*Alliaria petiolata* (M. Bieb.)).

Experimental Design

Each site consisted of 400-m^2 (20 by 20 m) paired deer exclosure and control plots, separated by a distance of <50 m. To exclude deer from exclosure plots, we erected 2.5-m-tall fencing with mesh openings of 15.2 cm surrounding the plots in August 2010. Each plot had a split-plot treatment of Amur honeysuckle removal or control. We removed honeysuckle from half (10 by 20 m) of each deer exclosure and control plot in 2010 by cutting each shrub at the base and applying a small amount of woody plant herbicide (Tordon, Dow AgroSciences, Indianapolis, IN) to the stem to hinder regrowth. The application of herbicide was limited to direct contact with the cut stems to reduce any accidental exposure to other plants. Herbicide application occurred during the initial removal of the honeysuckle in 2010, one year prior to sampling of ants. Additionally, ants have been found to have little response to broad application of foliar herbicides in forests (Scoriza et al. 2015); therefore, we did not expect herbicide application to have an effect on the ant community. In 2015, Amur honeysuckle basal area was 197 ± 20 m^2 ha^{-1} in honeysuckle present subplots; five years following removal, new establishment of honeysuckle was minimal with 15 ± 3 m^2 ha^{-1} basal area in honeysuckle removal subplots (C. H. and D. G., unpublished data). Deer density estimates at these sites ranged from 9.6 to 13.0 deer km^{-2} in 2013 (Barrett 2014), well above estimated historic densities of 3.1–4.2 deer km^{-2} in North America (McCabe and McCabe 1997).

Ant Sampling

We sampled ants in late May to early June from 2011 to 2014, a time when we expected highest abundance and richness of ants (Fellers 1989), as this is a period of moderate precipitation and temperature in the study region. We sampled ants using pitfall traps (hereafter referred to as pitfalls) and Winkler litter extraction (hereafter referred to as Winklers) at 12 sampling points at each site. Three sampling locations were placed in each 10- by 20-m subplot along a line 5 m from the subplot edge and at 5-m intervals. At each sampling location, we set a pitfall trap and sampled one 0.25-m^2 quadrat of litter adjacent to the pitfall. We collected 12 samples from each of the five sites during each year of the 4-yr study for both Winkler and pitfall samples, resulting in 60 Winkler and 60 pitfall samples each year and 240 samples of each collecting method during the study.

Pitfall and Winkler sampling occurred during the same interval when possible, with a maximum of 3 wk separating sampling methods at a given site in a given year. Pitfall traps consisted of a plastic specimen cup (5.5 cm in depth, 9 cm in diameter) inserted into the ground flush with the soil surface and partially filled with propylene glycol. For each sampling period, pitfalls were deployed in the field for 7 d. Pitfalls were covered with a raised board to prevent flooding from rain, and boards were held in place with angled iron stakes to prevent small mammal damage to traps. Pitfall locations were fixed throughout the study using PVC pipe to reduce digging-in effects (cups were nested inside the PVC when active).

Winkler samples were obtained by collecting leaf litter and woody detritus from a square 0.25-m^2 quadrat. The leaf litter and detritus were transported to the lab, placed in mesh bags, and hung inside the Winkler bags for 5 d to extract ants and other invertebrates. Prior to the study, we conducted multiple lab trials with extended extraction times but found little to no increase in yield of any invertebrates from leaf litter (K.U.C., unpublished data). In a similar system in which Winklers were used to collect ants, 3 d was the minimum for collecting the majority of the specimens in the litter sample (Ivanov et al. 2010). Litter collection was conducted at least 2 d following a major rain event, to increase extraction efficiency. All ant specimens were identified using Coovert (2005). Species length measurements were taken from Coovert (2005). Voucher specimens will be deposited at the Ohio State University Insect Collection.

Functional Groups

We used Ellison's (2012) functional group classification for ants in North American temperate forest ecosystems. Ant species were grouped into Subordinate Camponotini, Cold-climate Specialists, Cryptic Species, Opportunists, and Generalized Myrmicinae (Supp. Table 1 [online only]). Subordinate Camponotini are ecologically isolated from other temperate ant groups, owing to large body size and foraging patterns (Andersen 2000). Cold-climate Specialists are reliant on cool temperate regions, but are generally unspecialized in terms of diet. Cryptic Species are small species that nest and forage within the forest floor and logs. Opportunists are species that are dominant in areas with limited ant diversity, owing to disturbance or environmental stressors. Generalized Myrmicinae are species of *Crematogaster*, *Monomorium*, and *Pheidole* and are generally cosmopolitan and competitively dominant species (Andersen 2000). Our primary aim was to determine if different sampling methods led to significant differences in the frequency of occurrence of Opportunists and Cryptic Species, which are functional groups most often used in indicator studies. However, we also tested Cold-climate Specialists because they could potentially be used as early warning indicators of climate change. Additionally, we analyzed the response of Subordinate Camponotini, though this functional group is less studied as an indicator. We collected a single, uncommon species of Generalized Myrmicinae, so further analysis was not possible.

We hypothesized that ant functional groups would be differentially affected by deer and honeysuckle treatments through three mechanisms. First, homogenization of the plant community and reduction of understory cover owing to deer browsing and honeysuckle presence alters the understory habitat for ants. We predicted this would lead to increased frequency and diversity of Opportunists ant species. The negative impacts of deer and honeysuckle on native herbaceous plants were also predicted to decrease the abundance of *Aphaenogaster rudis* Enzmann, which is thought to be an important seed-dispersal mutualist for numerous understory plants. Second, deer and honeysuckle together alter leaf litter biomass, likely through nutrient deposition from deer and rapid decomposition of honeysuckle litter. A lower litter biomass in the presence of deer and honeysuckle would be predicted to decrease the diversity and frequency of Cryptic ant species. Third, honeysuckle shading of the forest floor decreases the surface temperatures in the understory. This might affect the frequency and diversity of Cold-climate Specialists, although more dramatic changes in broad climate conditions may be required to observe any changes in this group.

Statistical Analysis

We conducted two types of analyses on pitfall trap and litter samples. First, we compared the species composition and ant functional groups with pooled data across years, as sampling protocols were consistent across years. Second, we tested whether the ant species and community responses to deer and honeysuckle treatments differed between pitfall traps and litter samples separately by year, as we expected treatment effects to change across years. We only included ant workers in all analyses. We used several packages in the R programming language version 3.2.3 for statistical analyses (R Development Core Team 2015). Where appropriate, we inferred statistically significant differences among sampling methods or treatments when the null hypothesis was rejected with observed $P < 0.05$.

Sample Method Comparison

We calculated the sample frequency of individual ant species as the observed number of occurrences in either pitfall traps or litter samples divided by 240 pitfall traps or litter samples taken across 4 yr. We ranked and plotted frequency of each ant species for visual comparisons by trapping method (Longino and Colwell 1997, Ivanov and Keiper 2009). Two types of analyses were conducted that reflect the differences between overall species richness of a habitat and species density per unit of sampling (Gotelli and Colwell 2001). For overall richness, we compared observed and Chao1 estimates of species richness (Chao et al. 2005) and constructed rarefaction curves based on data pooled across all years for the two methods individually and combined (vegan package, R; Oksanen et al. 2016). Although there are drawbacks to most species richness estimators, Chao1 provides estimates of species richness with changes in sample size and is a conservative estimate of species richness (Hortal et al. 2006). Differences in species density by sampling method (Winklers, pitfalls, or combined) were compared within years using generalized linear mixed models (GLMM) with site as a random effect (glmer function, lme4 package, R; Bates et al. 2015) and a Poisson link function. For simplicity, we refer to analyses of species density of sample means as species richness, and comparisons of pooled data as overall species richness. We analyzed the frequency of occurrence of the four functional groups (Opportunists, Cryptic Species, Cold-climate Specialists, and Subordinate Camponotini) among sample units using one-way analysis of variance (ANOVA). Linear contrasts were conducted (glht function, multcomp package, R; Hothorn et al. 2008) when there were significant effects of sampling method in the overall model.

We conducted unconstrained ordinations on data pooled across years to test the effect of sampling method on observed ant community composition with Multidimensional Scaling (MDS) and Bray–Curtis dissimilarity (MDS and vegdist functions, vegan package, R; Oksanen et al. 2016). To test for differences in species composition among sampling methods, we used permutational multivariate analysis of variance (PERMANOVA; adonis function, vegan package, R) with site as stratum (Oksanen et al. 2016). We also examined whether sampling methods differed in within-group variability in species composition using analysis of multivariate dispersion (betadisper function, vegan package, R; Oksanen et al. 2016).

Analysis of Experimental Treatments

We analyzed the main and interactive effects of honeysuckle and deer treatments using split-plot ANOVA (lmer and glmer functions, lme4 package, R; Bates et al. 2015). Response variables were analyzed separately for each year and sampling method. Response variables included species richness, sample occurrence for separate functional groups, and *A. rudis* abundance. We analyzed *A. rudis* abundance, because this species had the highest frequency of occurrence in both sampling methods and is ecologically important to seed dispersal in eastern temperate forests (Ness et al. 2009). The response variables in the split-plot ANOVAs assumed different data distributions: a Gaussian function for log-transformed species richness and abundance of *A. rudis* and a binomial function for sample occurrence by functional groups. *F*-values are presented for log-transformed species richness and log-transformed abundance of *A. rudis*, while Wald *Z*-scores are presented for sample occurrence by functional groups.

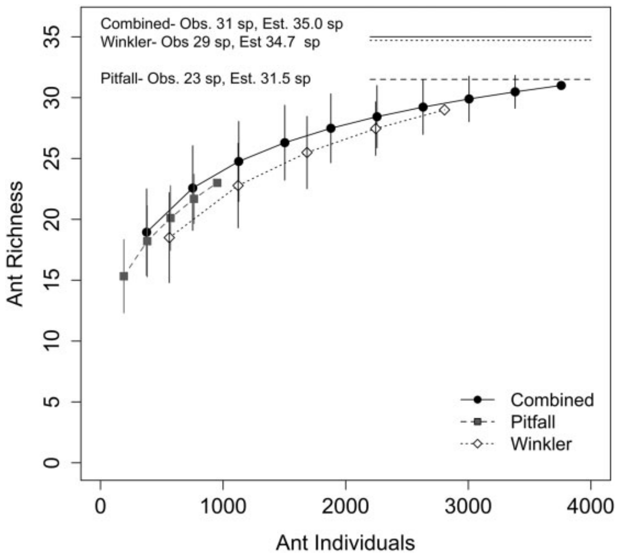

Fig. 1. Rarefaction curves of species richness by different sampling methods (Chao1 estimates for each method are given at location of the horizontal line). Error bars represent 1 S.E.

Results

Comparison of Sampling Methods

In total, 3,758 individuals comprising 31 species (Chao1 = 35) were collected using the combined sampling methods during the study (Fig. 1). Winklers collected more individuals and had higher overall species richness than pitfalls in all but one of the five sites across years (Supp. Table 2 [online only]). Rarefaction curves showed higher numbers of species per individuals collected in pitfall samples, but a higher asymptote in Winkler samples (Fig. 1). There were no differences in overall species richness between sampling methods (Winklers, pitfalls, or combined; $F_{2,12} = 2.53$, $P = 0.149$). The average body size of ants was smaller in Winklers (length, 3.73 ± 0.02 mm) compared with pitfalls (4.97 ± 0.07 mm). Winklers more closely approximated the overall ant abundance and overall richness (2,806 individuals, 29 spp., Chao1 = 35), collecting 94% of the total species, whereas pitfalls collected only 74% of the total species (952 individuals, 23 spp., Chao1 = 32; Fig. 1). Several uncommon species were collected by a single sampling method; however, two frequently collected species were only captured with a single method: *Tapinoma sessile* (Say) (Winklers) and *Lasius nearcticus* Wheeler (pitfalls). *Aphaenogaster rudis* was the most frequent ant in both sampling methods, but frequencies of other common species differed between methods (Fig. 2; Supp. Table 1 [online only]). Frequent species collected by Winklers were *Temnothorax curvispinosus* (Mayr), *Myrmica punctiventris* (Roger), and *Ponera pennsylvanica* Buckley (Fig. 2A), while *Camponotus chromaiodes* Bolton, *Lasius alienus* (Foerster), and *Stenamma schmittii* Wheeler were frequent in pitfalls (Fig. 2B). Multidimensional scaling ordination and PERMANOVA indicated that the ant community composition was different between Winklers and pitfalls ($F_{1,8} = 6.57$, $P = 0.007$, $R^2 = 45\%$), but there was no difference between Winklers and combined methods ($F_{1,8} = 0.78$, $P = 0.634$, $R^2 = 8.9\%$; Fig. 3). Analysis of multivariate dispersion showed no differences in the variation in species composition within pitfalls, Winklers, or combined samples ($F_{2,12} = 2.36$, $P = 0.136$).

The combined sample methods (Supp. Table 1 [online only]) collected 11 species of Opportunists (2,322 individuals), 6 Cold-

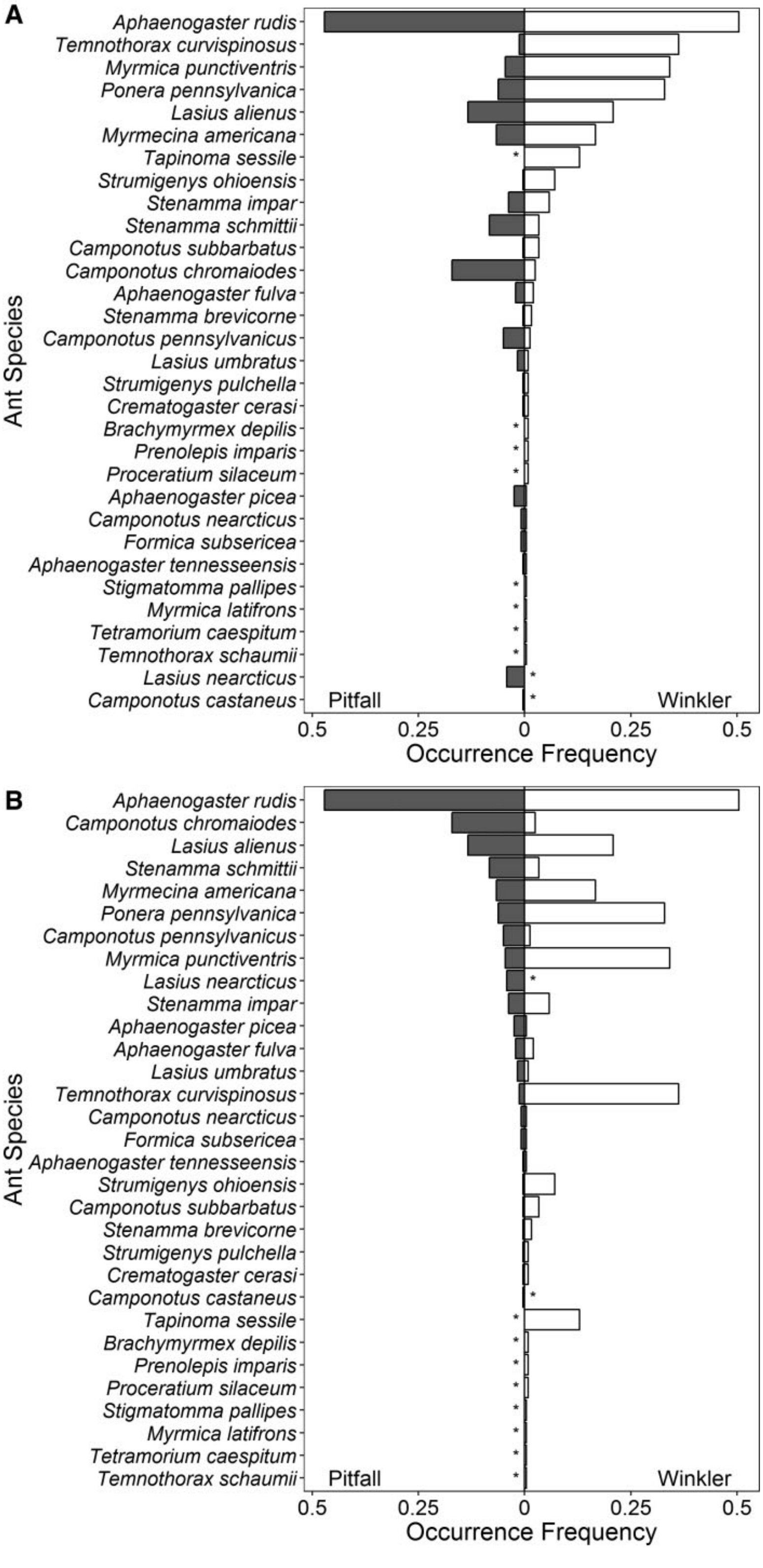

Fig. 2. Comparison of sampling methods using matched rank frequency plots. Species order standardized by (**A**) Winkler litter extraction and (**B**) Pitfall traps, oriented vertically with the most frequent species occurring at the top. Only two of the 10 singletons occurred in Winklers. Asterisks (*) designate zeros.

climate Specialists (759 individuals), 8 Cryptic Species (516 individuals), and 5 Subordinate Camponotini species (75 individuals). Winklers collected all 11 species of Opportunists and all 6 Cold-climate Specialists, 7 Cryptic Species, and 4 Subordinate Camponotini. Pitfalls collected 7 species of Opportunists, 5 Cold-climate Specialists, 5 Cryptic Species, and all 5 Subordinate Camponotini. Analysis of linear contrasts showed that there were no differences between combined methods and Winkler frequencies

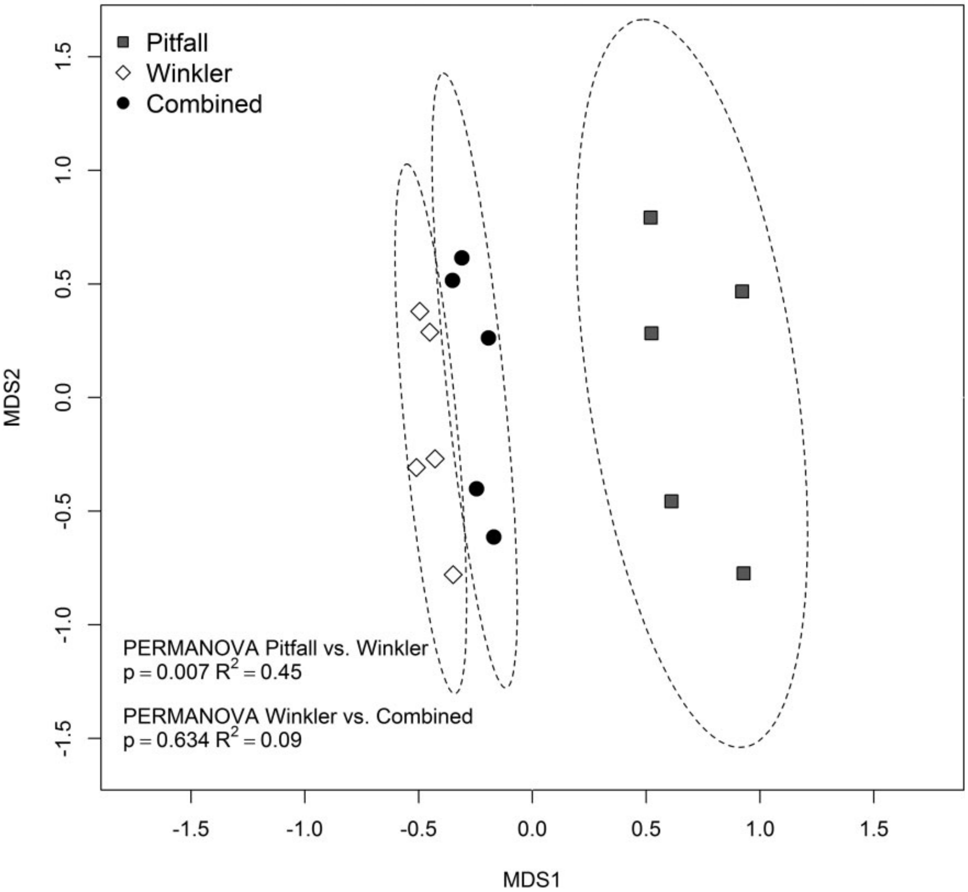

Fig. 3. Unconstrained MDS ordination showing differences in ant community composition among sampling. Dashed ovals represent 95% CIs.

of Cryptic Species ($T_2 = 1.27$, $P = 0.206$) and Opportunists ($T_2 = 1.45$, $P = 0.147$; Fig. 4). Pitfalls had lower trap frequencies than both combined methods and Winklers for Cryptic Species (combined–$T_2 = 7.16$, $P < 0.001$; Winklers–$T_2 = 5.89$, $P < 0.001$) and Opportunists (combined–$T_2 = 8.34$, $P < 0.001$; Winklers–$T_2 = 6.88$, $P < 0.001$; Fig. 4). Combined methods had higher sample frequencies for Cold-climate Specialists than pitfalls ($T_2 = 4.73$, $P < 0.001$) and Winklers ($T_2 = 2.45$, $P = 0.015$; Fig. 4). Pitfalls had higher frequencies of the Subordinate Camponotini functional group than Winklers ($T_2 = 3.93$, $P < 0.001$), but did not differ from frequencies based on the combined method ($T_2 = 1.12$, $P = 0.262$; Fig. 4).

Experimental Treatments

The effects of honeysuckle removal and deer exclosure on *A. rudis* abundance were inconsistent across years and significant in only a single year. Specifically, in 2012 pitfalls, we found a positive interactive effect of honeysuckle removal and deer exclosure on *A. rudis* abundance ($F_{1,8} = 13.28$, $P = 0.007$). We found a positive trend of *A. rudis* abundance in honeysuckle removal in 2013 for pitfalls ($F_{1,8} = 5.17$, $P = 0.053$). In 2014 Winkler samples, *A. rudis* abundance had a positive trend in deer exclosures ($F_{1,8} = 5.05$, $P = 0.055$) and there was a positive trend of *A. rudis* abundance in the interaction of deer exclosure and honeysuckle removal ($F_{1,8} = 4.40$, $P = 0.069$). We found no other significant differences for the main and interactive effects of treatment on ant richness (Table 1) or *A. rudis* abundance for either pitfalls or Winklers across years.

Ant functional groups did not respond consistently to deer and honeysuckle treatments. Deer exclosure had a negative effect on presence of Opportunists in 2012 for pitfalls ($Z = 2.09$, $P = 0.036$). In 2012 pitfalls, we found a positive trend of Opportunists in the interaction of honeysuckle removal and deer exclosure ($Z = 1.86$, $P = 0.063$). In 2013, for both pitfalls and Winklers, Cryptic Species presence had a negative trend in honeysuckle removal ($Z = 1.69$, $P = 0.092$; $Z = 1.66$, $P = 0.096$). In 2014, Cold-climate Specialists presence had a negative trend in honeysuckle removal for pitfalls only ($Z = 1.70$, $P = 0.090$). We found no other significant differences for the main and interactive effects of treatments on functional group presence across years.

Discussion

This study is among the first to compare sampling methods for ants in the context of a manipulative experimental design. To our knowledge, this study is also the first to use modified ant functional groups in temperate forests. Although we were unable to detect any significant impacts of sampling methods on the outcomes of the ecological experiment, we did find that the sampling method can affect measures of species richness and occurrence of some functional groups. Our results demonstrate that frequency data were similar when using combined methods compared with a single method for some functional groups (i.e., Winklers—Opportunists and Cryptic Species, and pitfalls—Subordinate Camponotini), but both of the methods alone underestimated the trap frequency of Cold-climate Specialists. Our results support the use of multiple sampling methods to measure species richness and composition if an inventory or monitoring Cold-climate Specialists is the goal. However, we found

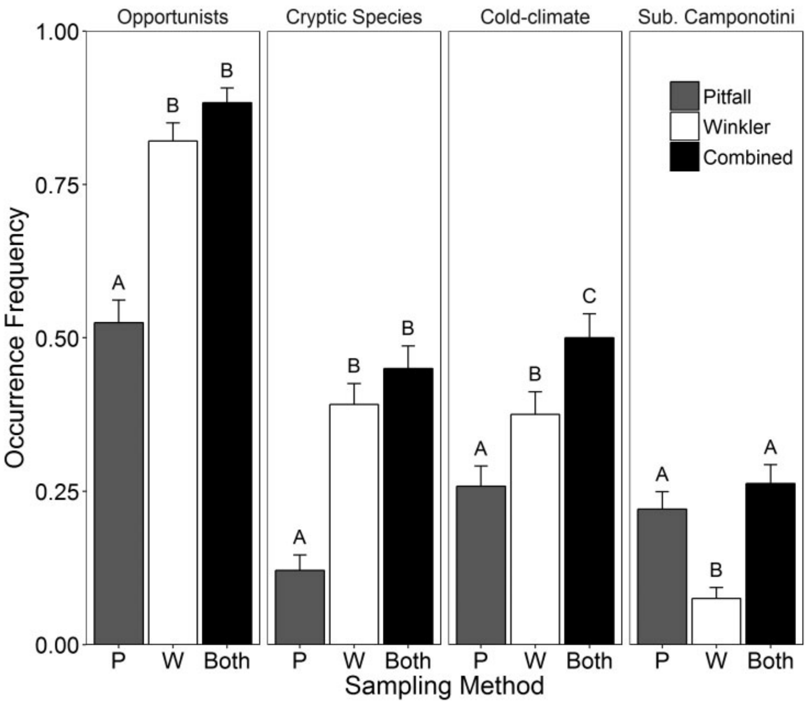

Fig. 4. Average frequency of occurrences in sampling the ant functional groups (Opportunists, Cryptic Species, Cold-climate Specialists, and Subordinate Camponotini). Letters indicate significant differences (linear contrasts; $P < 0.05$) in frequencies of ant functional groups among sampling methods. Error bars represent 1 S.E.

Table 1. Total abundance, mean abundance (± SE), total species richness, and mean species richness (± SE) for sampling methods for each experimental treatment

Sample	Treatment (deer, honeysuckle)	Abundance	Mean abundance	Species richness	Mean species richness
Pitfall					
	Control, Control	126	6.30 ± 1.24	14	2.95 ± 0.30
	Control, Removal	138	6.90 ± 1.23	14	3.10 ± 0.40
	Exclosure, Control	489	24.45 ± 17.50	15	2.75 ± 0.41
	Exclosure, Removal	199	9.95 ± 2.41	14	2.90 ± 0.40
Winkler					
	Control, Control	1,054	52.70 ± 18.90	16	7.70 ± 0.74
	Control, Removal	620	31.00 ± 6.97	20	6.95 ± 0.74
	Exclosure, Control	596	29.80 ± 5.60	19	7.85 ± 0.76
	Exclosure, Removal	536	26.80 ± 6.68	17	6.25 ± 0.62

Treatment refers to the four experimental treatments in our study: Deer control, Honeysuckle control; Deer control, Honeysuckle removal; Deer exclosure, Honeysuckle control; and Deer exclosure, Honeysuckle removal.

that Winklers alone are adequate for approximating overall species richness and composition, and the occurrence frequency of most functional groups, all of which are potentially valuable for ecological studies in terms of information gained per researcher time and expense.

Comparisons of Sampling Methods

Species Richness and Community Composition

Our findings that pitfalls collected fewer species than Winklers support the results of previous studies showing that Winklers are better suited than pitfalls for estimating overall species richness in temperate forests (Martelli et al. 2004, Lessard et al. 2007, Ivanov and Keiper 2009). Of the 31 total ant species collected in combined samples, 8 were unique to Winklers, whereas 2 were unique to pitfalls (Supp. Table 1 [online only]). Of the 8 species unique to Winklers, 7 were rarely collected (occurring in only 1 or 2 samples across all the years) because they are subterranean (*Stigmatomma pallipes* (Haldeman), *Brachymyrmex depilis* Emery, and *Proceratium silaceum* Roger), associated with forest edges (*Myrmica latifrons* (Stärcke)), arboreal (*Temnothorax schaumii* (Roger)), more common in cold seasons (*Prenolepis imparis* (Say)), or prefer open habitats with anthropogenic disturbance (*Tetramorium caespitum* (L.); Coovert 2005)). These species are small in body size, making them less likely to be captured in pitfall traps than Winkler samples (Kaspari and Weiser 1999, Parr and Chown 2001). The only species frequently (12% of samples) and uniquely found in Winklers was *T. sessile*, a species associated with anthropogenic disturbance that is not very common in wooded areas (Coovert 2005). When present, *T. sessile* often forms temporary nests at the surface of the soil–litter interface, which explains why this species was collected in the Winkler samples. Of the two species unique to pitfalls, one was collected in a single trap and is a large species more active at night (*Camponotus castaneus* (Latreille)), and the other was more frequently collected (4% of traps), but is primarily subterranean (*L. nearcticus*). *Camponotus castaneus* was only found in pitfalls, likely because litter collection occurred during the day, whereas pitfalls were deployed continuously for 7 d and nights. The collection of *L. nearcticus* only in pitfalls may be coincidental, as a previous study in a similar system in northeastern Ohio collected this species using Winklers (Ivanov and Keiper 2009).

The sampling methods yielded different views of the ant community (Fig. 3), and these differences are likely driven by differences in size, activity, and nesting habitats of the ants collected by each method. Consistent with previous studies (Olson 1991, Parr and Chown 2001, Ivanov and Keiper 2009), our results showed that Winklers yield smaller-bodied ant species compared with pitfalls. The higher abundance of smaller ants is likely a result of these ants being slower in their movements through the habitat compared with larger bodied ants, which increases their chance of occurrence in litter samples (Kaspari and Weiser 1999, Parr and Chown 2001). Differences in body size are primarily driven by high abundances of ants in the genus *Camponotus*, which were underrepresented in the Winklers (Fig. 2; Supp. Table 1 [online only]). Two previous studies (Ellison et al. 2007, Higgins and Lindgren 2012) found that ant species composition were similar between sampling methods; conversely, Wiezik et al. (2015) recorded differences in species composition between these sampling methods. In our study, the ant species composition in the combined methods were more similar to the Winkler samples, indicating that Winklers more closely approximated the entire community than pitfalls (Fig. 4). Moreover, ant community composition of pitfalls showed a nonsignificant trend for greater multivariate dispersion among samples compared with those of Winkler or the combined samples (Fig. 3), suggesting that pitfall trapping may be less consistent in sampling ant community composition, or that the activity density of different ant species is more variable among sites than the species composition of litter samples.

Functional Groups

The collection frequencies of multiple functional groups differed between sampling methods (Fig. 4). The high frequency of Opportunists in Winklers was likely driven by the high trapping frequency of *M. punctiventris* and *T. curvispinosus* in these samples (Fig. 2), both of which nest in leaf litter. As Cryptic Species nest in litter and woody detritus (Andersen 1997), have small body size, and lower vagility (Kaspari and Weiser 1999), these species are less likely to be encountered in pitfall traps, but are readily found in litter samples. Conversely, Subordinate Camponotini are larger and highly active species (Andersen 1997, Kaspari and Weiser 1999), some of which are nocturnal, and these species are more likely to be captured in pitfalls than in litter samples. Differences in litter depth or understory plant cover among sites likely drove differences in Cold-climate Specialists in pitfall traps and litter samples, and a combination of the methods resulted in higher occurrence than either method alone.

Experimental Responses

We found little to no support for our hypotheses and predictions on the effects of a keystone herbivore and an invasive shrub on ant species richness, *A. rudis* abundance, or occurrence of functional groups with either pitfalls or Winklers. Consistent with our results, previous studies have found little to no ant effects of deer (Bressette et al. 2012) or honeysuckle (Christopher and Cameron 2012). However, these results contradict the findings of Lessard et al. (2012), which found a positive effect of deer exclosure on ant abundance. Sample sizes were limited within treatments and years, which may have reduced our ability to detect the effects of experimental treatments. The ant community may also require longer time to show recovery following honeysuckle removal or deer exclusion. Unpublished data from the same experiment suggests deer and honeysuckle may play a role in altering the soil food web, leaf litter biomass, and decomposition rates, which may indirectly affect ant diversity and composition (Mahon et al. in preparation). Despite the lack of consistent and significant treatment effects, our findings of ant diversity and composition from the two sampling approaches should highlight the importance of selecting the proper method for targeting different components of the ant community in ecological studies involving manipulative experiments or comparisons among habitats differing in disturbance or other environmental factors.

Selecting the Appropriate Method

There are important limitations to both sampling methods when used in eastern temperate forests. In many areas, litter sampling and Winkler extraction cannot be used from mid-summer to early fall, because the litter layer is usually completely depleted by invasive earthworms (Holdsworth et al. 2012). Our study sites have been invaded by exotic earthworms, and, therefore, sampling is limited to spring, early summer, and late fall after leaf drop. On the other hand, pitfall traps are very time-consuming to install in the field and to sort in the lab, taking ∼30 min to sort or roughly twice as long as Winkler samples (M.B.M and K.U.C., unpublished data). Preservatives in pitfalls are attractive to mammals that subsequently destroy samples by upending the pitfall cups (requiring resetting the traps) or by infilling with soil. As pitfall samples are in the field for days in propylene glycol, DNA in these samples becomes degraded and specimens are unusable for subsequent molecular work, whereas specimens from Winkler extractions are immediately fixed in ethanol as they emerge from the litter.

Despite these shortcomings, each trapping technique provides a consistent, reproducible, and standardized method for collecting a large fraction of the ant community. Pitfalls are better at sampling larger, more vagile ants such as *Camponotus* spp., are more likely to collect ants with nocturnal activity, and can be used when a litter layer is absent. Additionally, pitfalls provide more species per individuals collected (Fig. 1), making this method more effective for rapid inventory assessments. Conversely, Winkler samples provide a measure of absolute density of ants (rather than activity density) and reduce digging-in and disturbance effects. Although Winklers yielded fewer species per sampled individuals (Fig. 1), the samples required less processing time. The disparity of sample processing time between Winkler and pitfall samples would be decreased with a larger litter sample (1 m^2 instead of 0.25 m^2; Bestelmeyer et al. 2000); but, larger, more vagile ant species would likely still evade capture. The ratio of species to individuals in Winkler samples would also likely be reduced with larger litter samples. The ratio of species to individuals is a concern in tropical systems, where many more ants must be pinned to ascertain species richness (Fisher 1999); however, in temperate regions with 10–20 species per site (Crist and Campbell, 2017), most ants are identifiable without mounting. If the goal of a study is to use ant functional groups as indicators of ecosystem disturbance and recovery, it may be important to focus on sampling methods that better characterize these groups. For example, based on our findings, studying the effects of climate change on Cold-climate Specialists would likely require both Winklers and pitfalls to detect these ant species. Conversely, only Winkler extraction would be required to assess the responses of Cryptic Species or Opportunists in manipulative experiments or comparisons across environmental gradients.

In conclusion, the use of one or both methods depends on whether the study goals are a species inventory or to identify the effects of ecosystem disturbance or stressor using ant community responses. Specifically, in eastern temperate forests, the use of Winklers is sufficient for collecting most ant species and a larger number of individuals, compared with pitfalls (Fig. 1; Ivanov and Keiper 2009). Moreover, ant communities collected by Winklers are representative of the overall ant community. However, if the response of ants in the genus *Camponotus* is of interest, pitfalls should be used. Our study was limited to epigaeic ant communities, whereas several species of *Camponotus* and *Formica* may extensively use the forest canopy, which may require other sampling methods such as canopy fogging.

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