

An evaluation of methods for sampling ants (Hymenoptera: Formicidae) in British Columbia, Canada

R.J. Higgins,¹ B.S. Lindgren

Abstract—Ants (Hymenoptera: Formicidae) are ubiquitous and of considerable ecological interest, yet poorly studied in Canada. Given their natural history attributes and relatively low density and diversity in cool boreal forests, there is a need to evaluate the applicability of commonly used approaches to sampling and analysis. We examined the relative utility of two pitfall trap designs, mini-Winkler litter extractions, and colony versus forager sampling for ecological studies. First, we found that Laurent (conventional) and Nordlander (modified to exclude larger nontarget organisms) pitfall traps were equally efficacious for estimating total species richness. Second, pitfall trapping yielded marginally higher total species richness than mini-Winkler litter sampling, by the incidence-based estimator (Chao2). Third, two studies considering the relationship between captures of individual ants in pitfall traps and identified ant colonies argued for caution in how pitfall captures are interpreted. In the first study, Nordlander traps placed in a grid surrounding nests of *Formica obscuripes* Forel revealed unique and highly patchy captures of individuals, with no patterns relating to proximity to the nest. In the second study, abundance estimates to compare ant assemblage structure in a simple grassland ecosystem by pitfall trapping (relative) and area-based hand sampling (absolute) for colonies, revealed that relative sampling does not reflect the absolute ant assemblage structure. Our results support, equivocally, the use of pitfall traps (Nordlander) over mini-Winklers in the cool moist forests of west-central British Columbia, but individual specimen counts should not be used when analysing the data.

Résumé—Les fourmis (Hymenoptera: Formicidae) sont ubiquistes et elles présentent un intérêt écologique considérable, mais elles demeurent peu étudiées au Canada. À cause des caractéristiques de leur histoire naturelle et de leur densité et diversité relativement basses dans les forêts boréales fraîches, il est nécessaire d'évaluer l'applicabilité des méthodologies d'échantillonnage et d'analyse couramment en usage. Nous examinons l'utilité relative de deux modèles de pièges à fosse, de mini-extracteurs de litière de type Winkler et de l'échantillonnage des colonies plutôt que des individus en recherche de nourriture dans les études écologiques. D'abord, nous trouvons que les pièges à fosse de Laurent (modèle courant) et de Nordlander (modifiés pour exclure les organismes plus grands non ciblés) sont tout aussi efficaces pour estimer la richesse spécifique totale. De plus, les pièges à fosse indiquent une richesse spécifique légèrement plus élevée que les mini-échantillonneurs de litière Winkler, au moyen de l'estimateur basé sur l'incidence (Chao2). Troisièmement, deux études qui examinent la relation entre les captures de fourmis individuelles dans les pièges à fosse et les colonies de fourmis identifiées soulignent la nécessité de prudence dans l'interprétation des captures dans les pièges à fosse. Dans la première étude, des pièges de Nordlander placés sur une grille entourant des nids de *Formica obscuripes* Forel produisent des captures uniques et fortement contagieuses d'individus, mais sans patron associé à la proximité du nid. Dans la seconde étude, les estimations d'abondance pour comparer la structure des peuplements de fourmis dans un écosystème simple de prairie avec des pièges à fosse (relatives) et par récolte manuelle des colonies par surface (absolues) montrent que l'échantillonnage relatif ne reflète pas la structure du peuplement absolu de fourmis. Nos résultats appuient, de manière équivoque, l'utilisation des pièges à fosse (Nordlander) plutôt que des mini-appareils Winkler dans les forêts fraîches et humides du centre ouest de la Colombie-Britannique, mais on ne devrait pas faire de décomptes des spécimens individuels dans l'analyse des données.

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Introduction

Sampling methodology is one of the first issues that require consideration in any ecological study. In Canada, few studies have considered ant (Hymenoptera: Formicidae) assemblages and although ubiquitous, ants often occur at low densities in cool moist forests (Higgins and Lindgren 2006). Ants in particular are challenging because colonies, the ideal unit for surveying this superorganism (Hölldobler and Wilson 2009), are often cryptic or embedded within a complex microlandscape, making identification difficult. Thus, by necessity, individual foragers are usually targeted for sampling. Prior to initiating ecological studies on ants it is important to consider sampling methodologies in the context of their natural history, as well as the data limitations associated with each technique (Bestelmeyer *et al.* 2000).

Pitfall trapping is a commonly used sampling methodology in ecological studies of ants. It is used for examining total species richness or assemblage structure and is recommended by the Ants of the Leaf Litter (ALL) Protocol (Agosti *et al.* 2000). Pitfall traps usually consist of a round cup partially filled with a preservative solution, and placed into the ground with the lip flush to, or just below, the surface (Laurent 1917; Woodcock 2005). Unfortunately, there is little standardisation in pitfall trap design, and discussion relating to tailoring the design to a particular fauna is lacking. Vertebrate bycatch is commonly a problem with the conventional Laurent design leading to both ethical issues and the spoilage of trap contents by vertebrate remains (Pearce *et al.* 2005).

The mini-Winkler litter extraction technique has been increasingly used in research on ground-dwelling ants, particularly for tropical ecosystems, and is also recommended by the ALL Protocol (Agosti *et al.* 2000). Mini-Winkler litter extractors are used to sample litter-associated ants from small fixed-area plots, usually 1 m² or less (Olson 1991; Agosti *et al.* 2000). The literature varies with respect to reports of the comparative efficacies of pitfall trapping and mini-Winkler litter extractions in estimating total species richness (Fisher 1999; Martelli *et al.* 2004; King and Porter 2005).

The interpretation of trap catches is also an issue that requires consideration, particularly for

pitfall trapping, given the natural history of ants. Some species form discrete, narrow trails leading directly to resource patches. These trails can be densely packed with travelling workers while immediate adjacent habitat is depauperate in ants (Sanders 1972; McIver *et al.* 1997). To date, this problem has not been widely recognised in the context of pitfall traps, but it is of critical importance if consideration is given to relative abundance values based on the number of individual ants captured by pitfall traps, as is frequently done (Savolainen and Vepsäläinen 1989; Bestelmeyer 2000; Dunn *et al.* 2007).

Our three research questions were the following:

1. Is there another trap design, equally efficacious to conventional pitfall traps, but better focused upon ants?

We compared the efficacies and biases of two pitfall trap designs (Laurent 1917; Nordlander 1987), with respect to species richness and ant size.

2. Are different sampling techniques more efficacious than pitfall trapping in sampling total species richness in cool moist forests?

We compared the efficacies of pitfall trapping and mini-Winkler litter sample extraction in estimating total species richness.

3. How do captures of individual ants in pitfall traps relate to ant colonies?

a) We examined the precision of captures of individual ants in pitfall traps by examining the distribution of ants in the immediate proximity of nests of the western thatching ant, *Formica obscuripes* Forel;

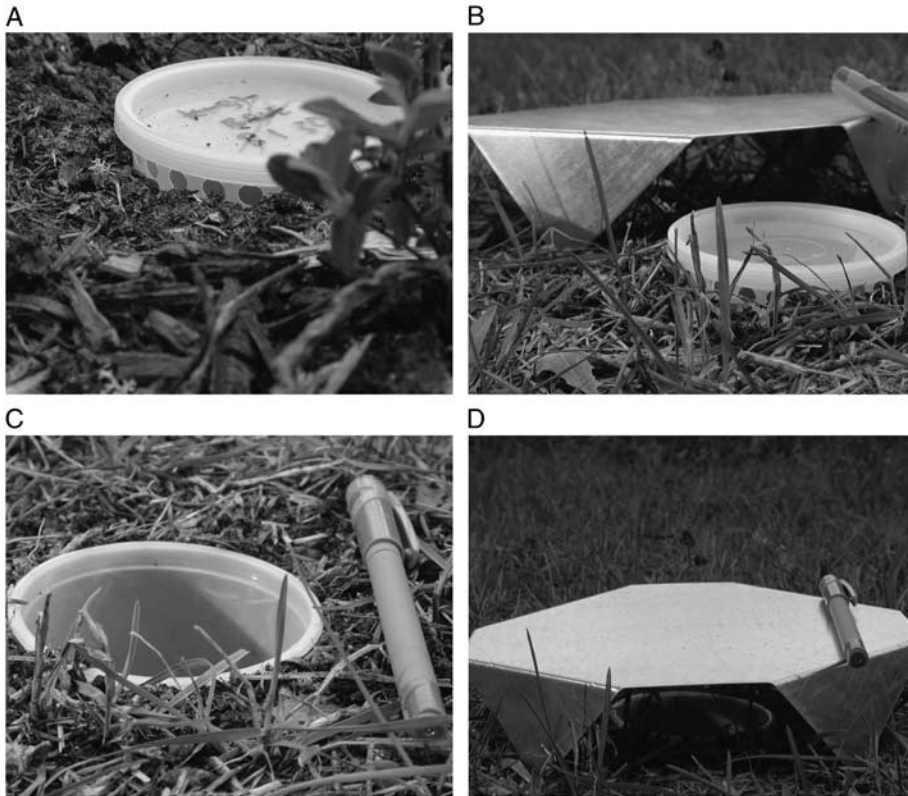
b) and, we determined if the apparent ant assemblage structure derived from a relative abundance estimation technique (pitfall trapping) is distinct from an absolute abundance technique (manual unit area sampling for ant colonies).

Methods

Pitfall trap design

We compared Nordlander (Nordlander 1987; Lemieux and Lindgren 1999) and conventional Laurent pitfall traps (Laurent 1917) (often called Barber pitfall traps (Barber 1931)), both with and without raised covers, with respect to sampling

Fig. 1. Pitfall trap designs tested at Topley, British Columbia. Each trap was filled with ~ 80 mL of preservative solution comprised of 25% propylene glycol and 75% water. Photos show: (A) Nordlander design with no cover (NNC); (B) Nordlander design with cover (NWC) (note: cover moved for purposes of illustration); (C) Laurent design with no cover (LNC); (D) Laurent design with cover (LWC). Pen provided for scale.



bias in ant size and total species richness (Fig. 1). Both Nordlander and Laurent pitfall traps consisted of 237 mL plastic cups (VWR Scientific Products, catalogue number 44333-002), used with an open top in the case of the Laurent but with a snap-on lid in the Nordlander configuration (Fig. 1). Following Bestelmeyer *et al.* (2000), these pitfall traps are of medium size with an inner diameter of 7.5 cm and a circumference of 23.6 cm. Ant access to the Nordlander traps occurred through ~ 25 holes (6 mm diameter) punched around the upper circumference just below the rim using a standard one-hole hand paper-punch. Ant access to the Laurent occurred simply by the insect falling over the open upper rim.

Holes to set the traps were dug using a narrow garden trowel, and for the Nordlander traps the cups were placed into the ground such that the

bottom of the holes were level with the surface of the soil/duff (Figs. 1A, 1B). A small amount of soil or moss was added to the top of the snap-on lid to reduce visibility to birds and mammals that might disturb the trap. Holes for setting the Laurent pitfall traps were slightly deeper, as these traps were positioned in the ground with the upper rim flush to the soil/duff surface (Fig. 1C). Raised covers consisted of a 20 cm square metal sheet with the corners bent down to hold the trap cover ~ 4.5 cm above the ground (Figs. 1B, 1D). A small amount of soil or moss was also added to the tops of the covers to reduce visibility to birds and mammals. Thus, four trap configurations were tested: Nordlander trap with no metal cover (NNC), Nordlander trap with metal cover (NWC), Laurent trap with no metal cover (LNC), and Laurent trap with metal

cover (LWC). Each trap was filled with ~ 80 mL of a solution of propylene glycol and water (25/75 by volume). Propylene glycol has a relatively low mammalian toxicity, with an LD₅₀ of 20 g/kg (oral rat) (Avantor 2008).

Trap designs were tested near Topley (54°28.8'N, 126°18'W, 1150 m), ~ 50 km east of Houston, British Columbia, Canada in a 15-year postharvest stand. The experimental plot was located in the subboreal spruce biogeoclimatic zone, moist-cool subzone, variant 2 (Meidinger and Pojar 1991) and was dominated by lodgepole pine (*Pinus contorta latifolia* (Engelmann) Critchfield) (Pinaceae).

We laid out traps in a randomised complete-block design. Ten replicates of each of the four trap configurations were laid out with a distance of 10 m between traps and 25 m between replicate blocks. Sampling was conducted over a 4-week period between 25 June and 23 July 2004. Catches in traps were collected twice, but were pooled for each individual trap for the analysis.

We identified ants collected from the pitfall traps in the laboratory (see section "Ant nomenclature and identifications" for details). Following identification, each ant was measured for alitrunk length (in lateral view; from the anterior point of the pronotum to the posterior point of the propodeum) and maximum head width (in dorsal view) to the nearest 0.1 mm using a calibrated 10X ocular scale on a dissecting microscope (model Nikon SMZ-2B). While head width is poorly related to ant size in some studies (Kaspari and Weiser 1999), it was not known if this would be true for northern fauna. Alitrunk lengths and head widths derived from all individuals, of any given species in any one pitfall trap, were averaged to reduce the risk that a few traps might skew the data due to oversampling a large number of worker ants on a foraging trail. Thus only one datum was used in the analysis for each species in a trap.

We tested the data for homogeneity of variance using Levene's test in STATA (Proc robvar) (STATA 9.2©1985–2007). Following this step, traps were compared for size bias in captures and differences in species richness by fixed-effects multiway ANOVA. Model variables included the trap type (Nordlander or Laurent), cover (with or without), interaction between trap type and cover, and replicate.

Pitfall trapping and mini-Winkler litter sampling

We sampled in three, 15-year postharvest sites within the subboreal spruce biogeoclimatic zone, moist-cold subzone, variant 2 (Meidinger and Pojar 1991) within 60 km of Houston, British Columbia (54°24'N, 126°40.2'W) between June and August of 2004. The distances between the three sites ranged from 25 to 78 km. The site age and time of year were chosen to coincide with maximal ant colony presence and activity based on previous research in the area (Higgins 2010). Within each site, we positioned a 1 ha sampling plot, so that contact with natural or anthropogenic boundaries (e.g., forest edges, streams, roads, etc.) was minimised. The 1 ha plot was laid out in a Cartesian coordinate 25 × 25 m grid to facilitate the location of randomly chosen sampling sites.

We set Nordlander pitfall traps (NNC configuration; Fig. 1A) along four transects, each comprised of five traps, each separated by 20 m, for a total of 20 pitfall traps. Transect initiation points and azimuths were randomly determined, but were not allowed to overlap. Traps were operated for two nonconsecutive 2-week periods between late June and early July and then late July and early August of 2004.

Mini-Winkler litter extraction bags (Marizete Pereira dos Santos, Bahia-Brasil, CEP 45 660 000, Brazil) consisted of an inner nylon mesh bag capable of holding ~ 2 L of sample with 4 mm openings. This mesh bag was suspended on a metal frame entirely within a larger cotton enclosure, closed at the top, which funneled into a lower collection cup filled with ~ 80 mL of a 25% propylene glycol solution in water.

We collected litter samples from 0.5 m² sampling areas at randomly chosen locations within the 1 ha plots. Ten samples were taken twice from each 1 ha plot between late June and August of 2004 with at least 2 weeks between subsequent sampling. We laid out a 0.5 m² frame at the randomly chosen sampling location, and surface material was scraped into the centre of the frame. Any twigs or clumps of earth were broken-up by hand and then filtered through a 1 cm² wire mesh within a sifting bag. Only material that passed through the sifting screen was used for the sample, which was then placed into a plastic bag and transported to the Houston

Forest Products mill, Houston, British Columbia. The sample was then added to the mini-Winkler bags and hung for ~ 48 hours in a shed where they were protected from rain and wind.

We derived the expected species accumulation curve (*i.e.*, the expected total species richness for any given subsampling effort within the full sampling protocol) using the rarified Mao Tau combinatorial algorithm (Mao *et al.* 2005) in EstimateS (Colwell 2006). This was then fitted to a nonasymptotic logarithmic function (see below) using SigmaPlot Version 9.0 (Systat Software Inc., San Jose, California, United States of America) to allow for extrapolation of the expected species accumulation dataset. Following Soberón and Llorente (1993), the logarithmic function $S(x) = 1/z \ln(1 + zax)$ was used to fit data, where x is the number of samples (pitfall traps or mini-Winkler litter extractions), $S(x)$ is the number of species accumulated at a given x (note: Soberón and Llorente (1993) described this equation as a function of sampling effort, specifically in units of time, here we use sample number as the unit of effort), and z and a are curve fitting parameters that control the rate of species accumulation. This model was then used to predict the number of samples required to add new species to the species list. In addition, the total species richness, as opposed to the observed species richness, was estimated by the incidence-based estimator, Chao2, using EstimateS (Walshur and Martin 2001; Colwell 2006). As sample size varied with technique (pitfall trapping, $n = 20$; mini-Winkler soil extractions, $n = 60$) due to other project objectives, each estimation for the pitfall traps was derived from 60 randomly drawn samples from the total dataset to match the mini-Winkler sample size.

Relating foraging ants to colonies: the spatial distribution of *F. obscuripes* ants

We examined the distribution of western thatching ant workers (*F. obscuripes*) in the immediate vicinity of their nest by sampling with Nordlander pitfall traps (NNC configuration; Fig. 1A). Five *F. obscuripes* nests, matched for approximate size and activity, were located on Becher's Prairie (51°58.2'N, 122°29.4'W, ~ 930 m). Becher's Prairie is a cattle-grazed grassland within the interior Douglas-fir biogeoclimatic zone, very dry-mild subzone (Meidinger and Pojar 1991) ~ 50 km west of Williams Lake,

British Columbia. We surveyed the area around each nest to ensure that no other nests of the same species were within 100 m. Selected nests were separated by distances ranging from 162 to 788 m (average 448 m). Nordlander pitfall traps were placed each 10 m within a Cartesian coordinate 40×40 m grid centred on the nest such that there were 24 traps in total (no trap was placed directly on the nest in the centre of the grid). These were set on 9–10 August 2002, and remained open for 14 days. Ants captured by the pitfall traps were identified in the laboratory (see section "Ant nomenclature and identifications" for details).

The total abundance of individual *F. obscuripes* captured was plotted spatially around the nest to qualitatively assess the pattern of distribution. The patterns arising from individual captures were visually assessed to determine if they were precise between nests. The range in captures for pitfalls equidistant to the nest was tabulated and examined for consistency.

Relating foraging ants to colonies: relative and absolute abundance estimates of ant assemblage structure

We compared the relative abundance estimates of ant assemblage structure derived from Nordlander pitfall trap (NNC configuration, Fig. 1A) sampling to absolute abundance estimates derived from hand sampling for ant colonies in a structurally simple grassland ecosystem at Becher's Prairie (see above for details). We laid out five Cartesian coordinate 12×12 m plots along a transect within homogeneous grassland devoid of trees, with 50 m separating each plot. Pitfall traps were spaced 2 m apart within the 12×12 m grids, with no trap closer than 2 m to the edge of the grid, for a total of 25 traps. Pitfall traps were set on 7–8 August 2002, and remained for 2 weeks.

Following pitfall trap removal, we intensively hand-sampled the 12×12 m grid for ants by lifting rocks and loosening vegetation. When ants were located, the number was recorded as one of three classes (Few: 1–5; Several >5 ; or Colony), and their position within the grid were recorded. Only ant species for which a colony identification was possible (*i.e.*, ant species which have colonies that may have multiple entrances spread across some area were excluded because of the difficulty in identifying a single colony) and only identifications of colonies

(i.e., where ant numbers were recorded as a 'colony' as opposed to 'few' or 'several') were included in the data analysis. For example, *Formica subpolita* Mayr, was frequently encountered during hand sampling but as this species may have deep nests with several access points within the grid, making identification of the number of colonies uncertain, they were not included in the data analysis. This was the only species recorded in this study that needed to be excluded. Counts were restricted to colonies because we observed that counts of individual ants can be highly variable depending upon weather. Further, as the colony is conceptually the unit of organisation (Hölldobler and Wilson 2009), it is a more appropriate metric for assessing ant density. Thus, the total colony counts by species, per 12 × 12 m sampling grid, were used to calculate the absolute assembly structure.

We assessed the relative proportions of each ant species both by simple presence or absence in pitfall traps and by the total number of individual ants of a given species in all traps in each plot. In the former, if 11 out of 25 pitfall traps contained a given species, that species was initially recorded as 0.44, which was then adjusted as a percentage of the total ant fauna for that plot. In the latter, the total number of individuals of a given species in all pitfall traps in each plot were tallied and then expressed as a percentage of the total ant fauna for that plot. Absolute abundances were assessed by total counts of colonies per unit area that were then adjusted to a percentage of the total ant fauna per plot.

Data for each species were tested for homogeneity of variance using Levene's test in STATA (Proc robvar) (STATA 9.2[©]1985–2007) then compared across the three-sampling/tallying techniques (i.e., absolute versus presence/absence in pitfall traps; absolute versus total abundance in pitfall traps; presence/absence versus total abundance) by one-way ANOVA. Tests for differences between the three pairwise sampling/tallying techniques were performed using a *post-hoc* Bonferroni test (STATA 9.2[©]1985–2007) when the *F*-value was significant.

Ant nomenclature and identifications

We followed ant species nomenclature as revised by Bolton *et al.* (2006) except where more recent revisions have been made. We identified

ants to species using the keys of Wheeler and Wheeler (1963), Francoeur (1973), Wheeler and Wheeler (1986), Naumann *et al.* (1999), and Hansen and Klotz (2005). Ants of the genus *Myrmica* were identified using an unpublished key provided by A. Francoeur (Centre de données sur la biodiversité du Québec, Chicoutimi, Québec). Voucher specimens will be deposited before 2013 with the Curator of Entomology at the Royal British Columbia Museum.

Results

Pitfall trap design

Eleven species of ants in four genera were identified in all trap types (Table 1). The genus *Formica* was the most common, with six species, but *Myrmica alaskensis* Wheeler (Myrmicinae) was the most commonly collected ant species. A mean of 2.5 species were collected per trap (Table 2) across trap types, and a total of 516 ants were collected over the 4-week sampling period.

Both model factors (i.e., trap type (Nordlander or Laurent) and cover (with or without)), showed statistically significant differences in species richness, but there was also a significant interaction between trap type and cover ($F = 5.27$; $df = 1,38$; $P = 0.003$). This interaction was due to a reduction in catch caused by the raised cover when used with the Nordlander trap, reducing captures from a mean of 2.8 species to 1.6 species. The cover had no significant effect on the Laurent trap captures (Table 2).

Head width and alitrunk length correlated strongly ($r > 0.9$). Given the disproportionate caste-related variability in head width that does occur in some genera of Formicidae (Hölldobler and Wilson 1990), and the observation that head width has been shown to be a poor indicator of overall ant size (Kaspari and Weiser 1999), only alitrunk length was used to assess trap type size bias. ANOVA indicated no significant differences for alitrunk length between trap types (Table 2) (trap type: $F = 0.75$; $df = 1,16$; $P = 0.395$; cover: $F = 0.08$; $df = 1,16$; $P = 0.784$; trap type and cover interaction: $F = 1.45$; $df = 1,16$; $P = 0.239$).

Pitfall trapping and mini-Winkler litter sampling

Nordlander pitfall trap sampling yielded the greatest number of collected species (Mao Tau),

Table 1. Ant species captured (indicated by total captures of individuals) by each of four pitfall trap designs near Topley, British Columbia.

Species	Nordlander		Laurent	
	With no cover (NNC)	With cover (NWC)	With no cover (LNC)	With cover (LWC)
<i>Camponotus herculeanus</i>	32	8	26	71
<i>Formica accrete</i>	12	3	7	12
<i>Formica argentea</i>	4	0	6	2
<i>Formica aserva</i>	76	34	11	8
<i>Formica fusca</i>	1	0	2	0
<i>Formica hewitti</i>	0	0	1	1
<i>Formica neorufibarbis</i>	8	7	5	6
<i>Leptothorax muscorum</i>	0	1	1	4
<i>Myrmica alaskensis</i>	44	30	37	37
<i>Myrmica fracticornis</i>	2	1	0	7
<i>Myrmica incompleta</i>	5	0	2	2
Total species richness	9	7	10	10

The four pitfall designs were laid out randomly within ten replicate blocks, which were sampled twice. Traps were put in place on 25 June and sampled on 9 and 23 July 2004. Although total abundance data are provided, analyses were performed on presence/absence data.

Table 2. Mean alitrunk length and mean number of ant species collected (\pm SE) in each of four trap combinations in Topley, British Columbia.

Trap design	Cover	Trap code	<i>n</i>	Mean alitrunk length (mm) (\pm SE)	Mean number of species per trap (\pm SE)
Laurent	Yes	LWC	10	2.1 (0.13)	2.8 (0.28)
Laurent	No	LNC	9	2.0 (0.15)	2.8 (0.35)
Nordlander	Yes	NWC	10	1.8 (0.20)	1.6 (0.21)
Nordlander	No	NNC	10	2.0 (0.13)	2.8 (0.33)
All traps			39	2.0 (0.07)	2.5 (0.17)

Traps were laid out on 25 June 2004 and sampled on 9 and 23 July. Number of sample traps = *n*. Variance in the number of sample traps arises from animal disturbance or unrelocated traps.

as well as total estimated species (Chao2) when compared to mini-Winkler soil-litter sampling (Fig. 2). An estimate of 11 species (95% CI: 11, 11) from 60 Nordlander pitfall samples, as compared to 9 species (95% CI: 9, 9.02) for equivalent sampling with mini-Winklers, arose from Chao 2 analyses, indicating a small but significant difference. Following the logarithmic function modelled to the expected species accumulation curve (Table 3), it is estimated that an additional 53 Nordlander pitfall samples would be necessary to add one more species while mini-Winkler soil-litter sampling would require 42 more samples.

Relating foraging ants to colonies: the spatial distribution of *F. obscuripes* ants

The distribution of *F. obscuripes* individuals in the immediate vicinity of their nests was unique to each nest and highly patchy (Fig. 3), failing to indicate any pattern relative to their proximity to the nest. Areas of most concentrated captures differed for each nest. Most of the nests included large areas within the 40 \times 40 m grid in which no *F. obscuripes* ants were captured despite a relatively close proximity of the traps to the nest. In particular, Nest 2 (Fig. 3) collected only a single *F. obscuripes* ant in all grid pitfall traps despite observed worker

Fig. 2. Expected species accumulation curve (Mao Tau), fitted logarithmic function ($S(x) = 1/z \ln(1 + zax)$) to the expected species accumulation curve, and incidence-based estimator (Chao2) approximation of total ant species richness derived from 60 Nordlander pitfall traps and 60 mini-Winkler litter samples collected in 2004. Sampling was performed in three, 15-year postharvest pine forest plots (subboreal spruce biogeoclimatic zone, moist cold subzone, variant 2 (Meidinger and Pojar 1991)). Mao Tau curve and Chao2 data calculated using EstimateS (Colwell 2006) while the logarithmic function follows Soberón and Llorente (1993).

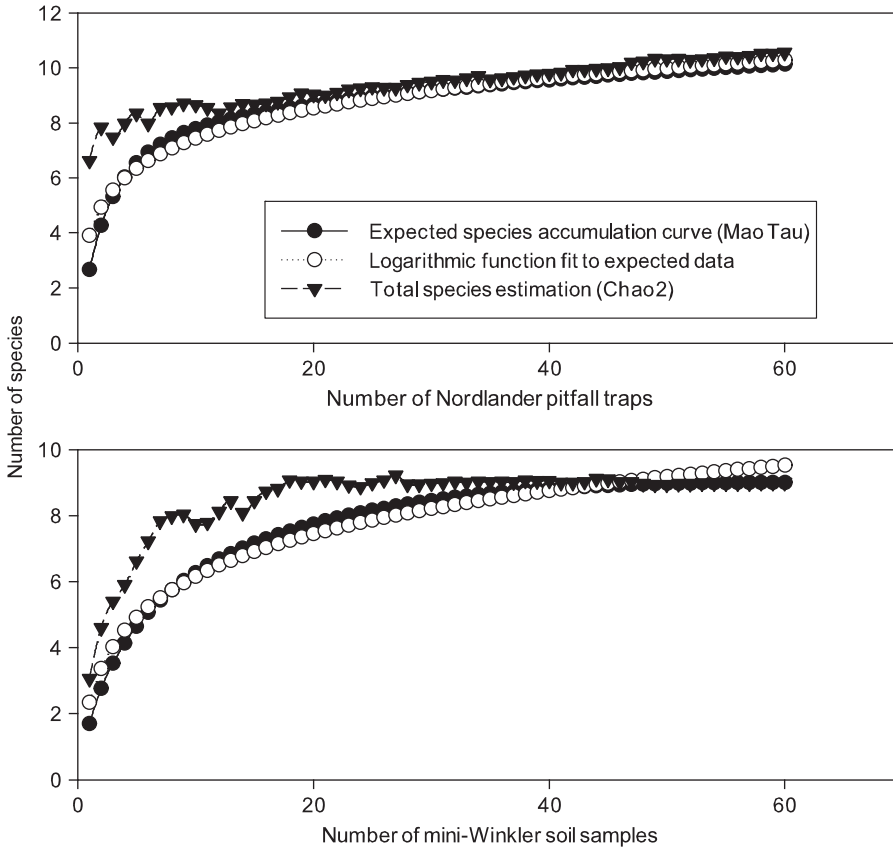


Table 3. Logarithmic parameters ($S(x) = 1/z \ln(1 + zax)$), statistical fit (t statistic derived from null hypothesis in which model parameters (i.e., z , a) is considered zero; P -value is probability of null hypothesis being accepted), and extrapolation of an observed mean species accumulation curve (Mao Tau, EstimateS) derived from Nordlander pitfall trap samples and mini-Winkler litter extraction samples ($n = 60$).

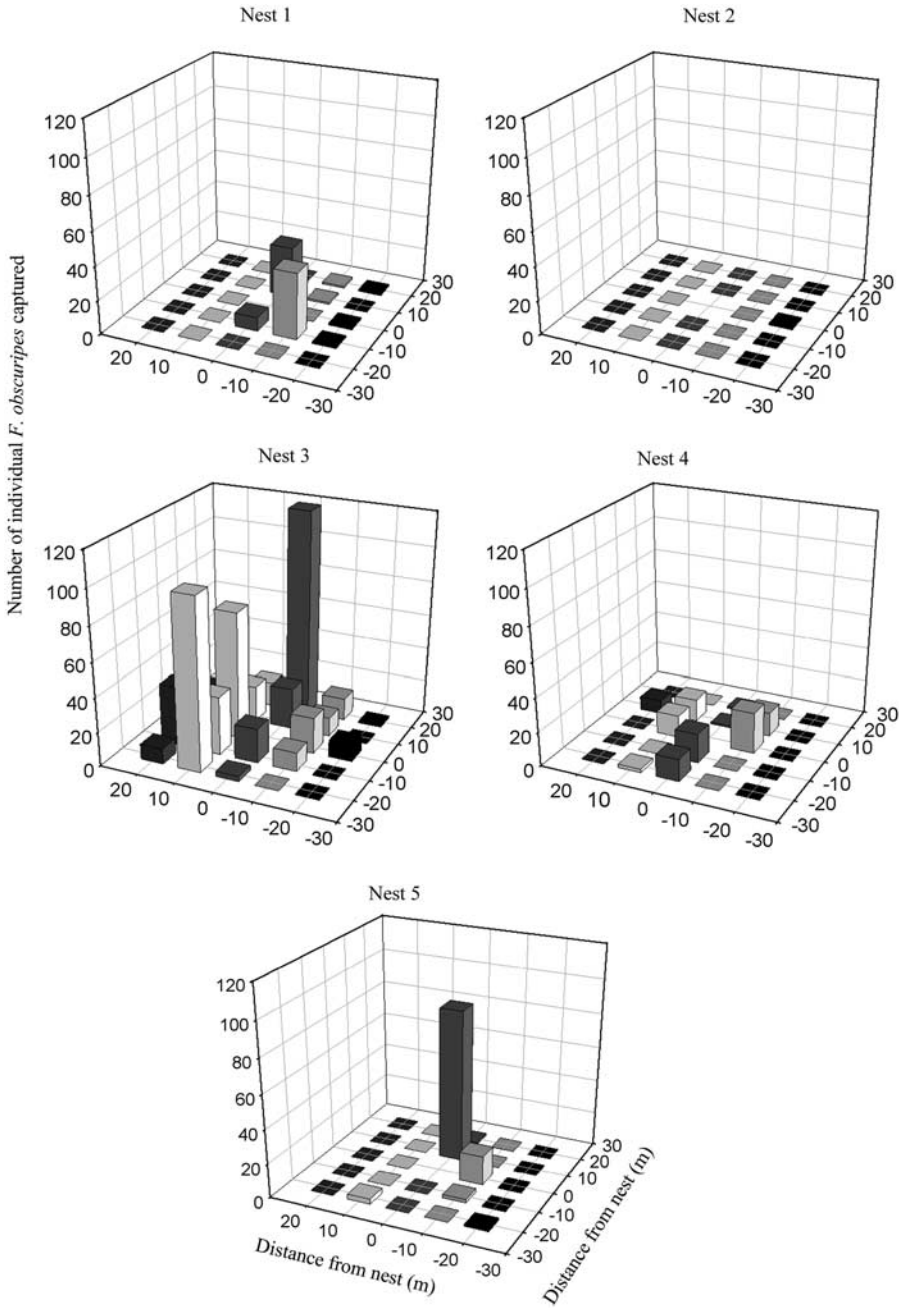
	Parameter	Estimate	SE	t statistic	P -value
Nordlander pitfall trap ¹	z	0.6284	0.0153	41.057	<0.0001
	a	16.8924	1.9076	8.8554	<0.0001
Mini-Winkler litter extractor ²	z	0.5227	0.0143	36.6645	<0.0001
	a	4.5953	0.4105	11.1934	<0.0001

Samples collected within 60 km of Houston, British Columbia, between June and August 2004.

¹ $R^2 = 0.9712$; adjusted $R^2 = 0.9707$; standard error estimate = 0.2477; estimated number of species at 60 samples = 10.27; estimated number of additional samples, beyond 60, necessary to add one additional species = 53.

² $R^2 = 0.9727$; adjusted $R^2 = 0.9722$; standard error estimate = 0.2814; estimated number of species at 60 samples = 9.52; estimated number of additional samples, beyond 60, necessary to add one additional species = 42.

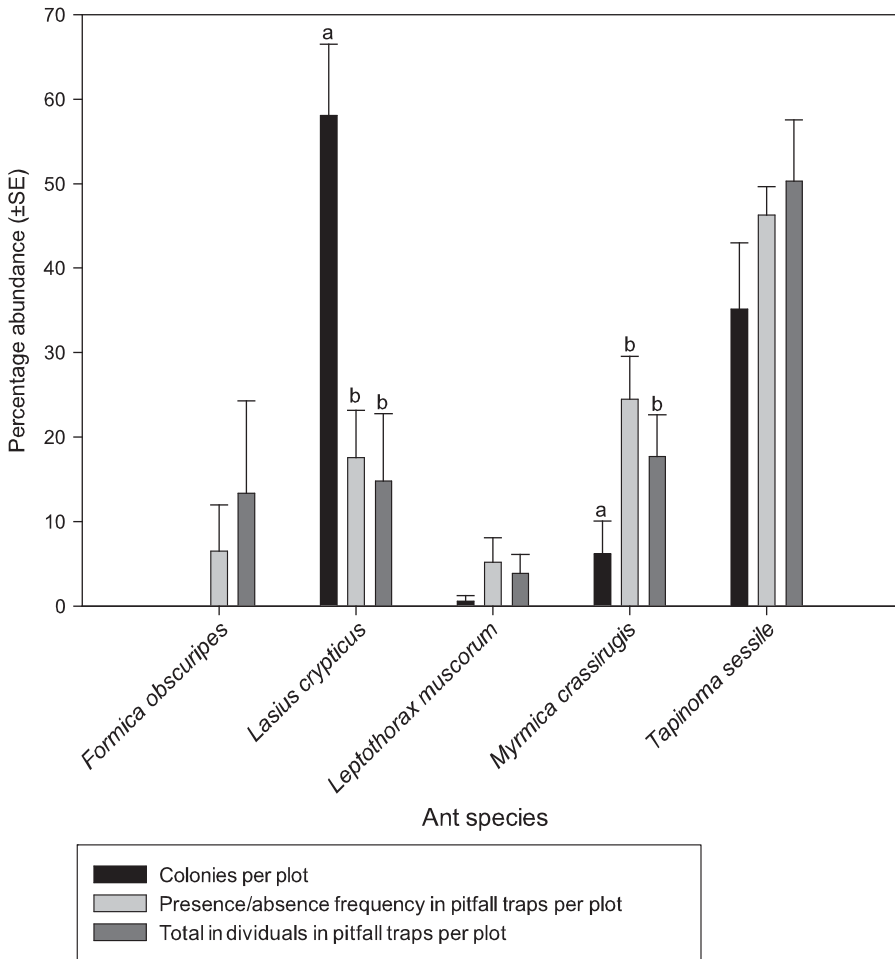
Fig. 3. Three-dimensional column plots of the distribution of captured individual *Formica obscuripes* ants in Nordlander pitfall traps around five established nests at Becher’s Prairie, a grassland ecosystem, in 2003. The nest is in the centre position (0,0), in each plot. Nordlander pitfall traps were laid out each 10m within a Cartesian 40 × 40 m grid for 14 days. Differing shade tones are used for visual contrast and do not represent any differences in the manipulated variable.



activity, on and around the nest, appearing similar in activity to the other nests. Pitfall traps 10m apart varied greatly in the number of indi-

viduals captured. In one case, one trap collected 120 ants while an adjacent trap, 10m away, collected only 13 (Fig. 3, Nest 3). The maximum

Fig. 4. Apparent assemblage structure, expressed as percentage abundance, of five species of ants at Becher’s prairie, a grassland ecosystem, derived from relative and absolute abundance sampling of five 12 × 12 m plots in 2003. Relative abundance estimates (presence/absence frequency and total individuals per plot) were made using Nordlander pitfall traps, which were laid out in a Cartesian grid each 2 m within each plot. Pitfall traps operated over a period of 2 weeks. Absolute abundance estimates (colonies per plot) determined by hand sampling of the plots. Letters indicate significant differences between sampling categories.



range in captures across the 24 pitfall traps at each nest overall was: Nest 1, 39; Nest 2, 1; Nest 3, 120; Nest 4, 24; Nest 5, 89.

Relating foraging ants to colonies: relative and absolute abundance estimates of ant assemblage structure

Six species of ants, *Tapinoma sessile* (Say) (Dolichoderinae), *Lasius crypticus* Wilson, *F. obscuripes* Forel, *F. subpolita* Mayr (Formicinae), *Leptothorax muscorum* (Nylander), and *Myrmica crassirugis* Francoeur (Myrmicinae) were identified

from the five 12 × 12 m plots laid out in this study. All six species were identified from both pitfall trap sampling and hand sampling. Of these, *F. subpolita*, was excluded from the final analysis as indicated in the section “Methods”.

The abundance determination of species within the ant assemblage varied with both the sampling and analytical technique used to count ants and species (Fig. 4). The most common ant collected in Nordlander pitfall traps (relative abundance), either assessed as simple presence/absence per trap per plot or in total individuals in

all traps per plot, was *T. sessile*. The most common ant species identified by hand sampling (absolute abundance) was *L. crypticus*. *Leptothorax muscorum* was the least common species, by all methodologies. No colonies of *F. obscuripes* were identified during hand sampling of the plots, but this species did turn up in traps in two of the plots that were ~ 130 and 100 m from the nearest identified *F. obscuripes* nest.

Comparison of hand sampling (absolute abundance) to presence/absence per trap and total individuals in all traps (relative abundance) per plot by one-way ANOVA indicated a species-specific relationship. There were no significant differences between absolute or relative abundances for *F. obscuripes* ($F = 0.89$; $df = 2,12$; $P = 0.49$), *L. muscorum* ($F = 1.21$; $df = 2,12$; $P = 0.33$) or *T. sessile* ($F = 1.47$; $df = 2,12$; $P = 0.27$). Hand sampling (absolute abundance), for *L. crypticus*, resulted in an abundance of just under 60% of the total assessed fauna, while pitfall trapping, by either simple presence/absence tallies or total individuals, indicated a relative abundance of under 20% (Fig. 4). For this species, ANOVA across the three-sampling/tallying techniques did indicate a significant difference ($F = 10.61$; $df = 2,12$; $P = 0.002$) arising from two pairwise comparisons between absolute assemblage composition and both hand sampling and total individuals per plot (*post-hoc* Bonferroni, $P = 0.007$ and $P = 0.004$, respectively). Analysis of *M. crassirugis* across the three-sampling/tallying types also indicated a significant difference between groups ($F = 3.98$; $df = 2,12$; $P = 0.05$). Here the absolute assemblage composition for *M. crassirugis* was ~ 6.2% as compared to an estimate of 24.5% derived from tallying presence/absence from pitfall traps (*post-hoc* Bonferroni, $P = 0.05$) (Fig. 4). No significant difference was noted between hand sampling and total individuals in all traps per plot (*post-hoc* Bonferroni, $P = 0.34$).

Discussion

Pitfall trap efficacy

Pitfall traps were first described in the literature by Laurent (1917) although they are sometimes referred to as Barber traps (Barber 1931; Lemieux and Lindgren 1999). They are especially popular with entomologists working with epigeaic

invertebrates because they are inexpensive, easy to install, and sample 24 hours a day (Agosti *et al.* 2000; Schlick-Steiner *et al.* 2006).

The Nordlander pitfall trap design has been compared to the conventional Laurent design by both Lemieux and Lindgren (1999) and Pearce *et al.* (2005), although not in the context of sampling for ants, or for examining the effect of trap cover. Pearce *et al.* (2005), focusing on Carabidae (Coleoptera) and spiders (Araneae), found the Nordlander captured fewer individuals than conventional designs but captured more species. Lemieux and Lindgren (1999), examining Carabidae, found Nordlanders and conventional pitfalls were 70% similar in the assemblage sampled and only differed significantly with respect to two species, with each trap type performing preferentially for one of these two species.

The significant interaction between pitfall trap design (Nordlander or Laurent) and the presence or absence of a cover, indicated an effect on the number of species sampled. Both trap design and cover combined such that the Nordlander trap with cover sampled the least species as compared to all others (Table 2). In practice, however, the Nordlander trap is used without a separate cover, making it equally efficacious (Table 2) to the conventional Laurent trap with cover, reducing concerns about trap efficacy. In a preliminary, five-replicate experiment of the same trap design configurations carried out in a different biogeoclimatic zone and with a different ant assemblage, we found no significant effect for any aspect of trap design. These data were excluded because of frequent trap disturbance by vertebrates, resulting in low sampling power. Nevertheless, these results confirmed that the Nordlander trap is suitable for sampling of ants in cool, temperate environments.

Despite the significant effect for species richness arising from the trap and cover interaction, no effect was noted for ant size (alitrunk length), suggesting that trap designs did not differ with respect to their size bias. Pitfall traps have been shown to be activity biased, with faster, usually larger species more frequently sampled (Lang 2000; Hancock and Legg 2011). This was an initial and fortunately unfounded concern, given the possibility that a fast moving ant might avoid the more visible Nordlander trap or that large ant might perceive a 6 mm hole as constricting and therefore also avoid an interaction.

Although Pearce *et al.* (2005) reported difficulty installing the Nordlander design in the field, we found that it was no more difficult to install than conventional pitfall traps. The Laurent design normally includes a physically separate cover fashioned from various materials (*e.g.*, wood, metal, plastic, etc.) to protect the trap from flooding during rainfall and reduce evaporation of the trapping fluid. These covers can be bulky and cumbersome to carry in the field, particularly if high numbers of traps are used. As the Nordlander trap has lid integrated in the design, fieldwork can be simplified.

While a robust literature related to pitfall trapping exists (Greenslade and Greenslade 1971; Work *et al.* 2002; Vogt and Harsh 2003; Phillips and Cobb 2005), the problem of vertebrate bycatch is largely ignored. Conventional open pitfall traps, here called Laurent traps (Laurent 1917), can easily trap small vertebrates. The Nordlander pitfall trap (Nordlander 1987; Lemieux and Lindgren 1999; Pearce *et al.* 2005) may provide a solution to this problem. As designed for this study, the only access is through the 6 mm holes, which should be large enough for all ants but too small to allow for vertebrate bycatch. No vertebrates were captured in any of the trap designs used in this study, so their relative performance could not be directly assessed. Additional and extensive use of the Nordlander design as described by Higgins (2010) and McColl (2010) were also free of vertebrate bycatch. As vertebrate bycatch is a concern for institutional ethics committees in Canada operating under the guidelines established by the Canadian Council on Animal Care (CCAC 2007), the Nordlander pitfall trap is advantageous.

Pitfall trapping and mini-Winkler litter sampling

The need to rapidly assess the total species richness of a given taxon in a defined area is central to many ecological- and conservation-based studies. Although a wide variety of techniques exist, three are particularly common in the myrmecological literature. These are pitfall trapping, litter extraction (of which the mini-Winkler extractor is very common), and baiting (Bestelmeyer *et al.* 2000). The use of baits was found to be untenable in the low-density ant assemblages typical in the cool-moist, subboreal

forests of west-central British Columbia. Several attempts with randomly placed baits during the course of our study failed to attract any ants over a period of 30 minutes. Pitfall traps and mini-Winkler litter extractions are, however, potentially viable sampling methodologies for estimating total species richness in these forests.

Most studies have shown both mini-Winkler litter sampling and pitfall trapping to produce unique species (Fisher 1999; Martelli *et al.* 2004; King and Porter 2005), although the mini-Winkler species assemblage, in our study, was entirely a subset of the pitfall trap assemblage. Nordlander pitfall trapping was shown to be more efficacious in both actual (*i.e.*, Mao Tau) and estimated total species richness (*i.e.*, Chao2) although the differences were not large (1–2 species for Mao Tau and Chao2, respectively). Logarithmic modelling of the Mao Tau species accumulation curve indicated, however, that it would require 42 additional litter samples to add one more species to the species list while it would take 53 additional Nordlander pitfall trap samples. This is likely because the asymptote of the logarithmic model for the mini-Winkler extractions does not appear to be as close to approaching a zero slope as is the case for the Nordlander pitfall samples (Fig. 4).

To our knowledge there has been only one study assessing the efficacy of pitfall traps and mini-Winklers in cool forests (Austria) (Tista and Fieldler 2011). This work, as with ours, found that pitfall trapping was superior to mini-Winklers in sampling for total species richness, although to a greater degree than our own. It should be noted, however, that Tista and Fieldler (2011) used pitfall traps baited with honey and rum unlike our nonbaited pitfalls. The literature, though, is not consistent with respect to the performance of these two trapping techniques, and two factors may be important. First, pitfall trapping appears inferior to mini-Winkler litter sampling in tropical ecosystems where a well-developed litter fauna exists. For example, in the tropical rainforests of eastern Madagascar one study recovered five times the number of species using mini-Winklers as compared to small pitfall traps (18 mm diameter) (Fisher 1999). Second, in more temperate ecosystems mini-Winklers may appear superior to pitfall traps where the length of time pitfall traps remain in the field is short.

For example, in temperate hardwood and pine forests in Tennessee (United States of America) litter sifting yielded 1.2–2.5 times the number of species as pitfall traps (Martelli *et al.* 2004), a result similar to hardwood forests in Ohio (Ivanov and Keiper 2009). The poor performance of pitfall traps in these studies may have arisen from the relatively short period of trapping (48 and 72 hours, respectively). We trapped for a 2-week period, following Lemieux and Lindgren (1999), who used the same trap design (albeit larger) and operated in similar habitats.

Relating foraging ants to colonies: the spatial distribution of *F. obscuripes* ants

The information derived from the trapping of epigeaic invertebrates is normally considered suitable for determination of relative abundance information (Southwood and Henderson 2000). These data may be calculated from tallies of total individuals or from simple presence–absence (incidence) observations. It is common in the myrmecological literature for tallies of total individuals captured to be used to derive relative abundance data (Savolainen and Vepsäläinen 1989; Bestelmeyer 2000; Parr and Chown 2001; Wang *et al.* 2001a; Schowalter *et al.* 2003; Borgelt and New 2005; Dunn *et al.* 2007). The natural history of ant species and the manner in which they are distributed in the environment, however, should make myrmecologists wary of this approach.

Ants are social insects that usually create permanent to semi-permanent nests from which they forage. Foraging often results in the identification of resource-rich patches (*e.g.*, honeydew producing aphids) to which the colony recruits a great number of workers, frequently along well-established trunk trails reinforced by pheromones (Sanders 1972; Hölldobler and Wilson 1990; McIver and Yandell 1998). This is especially the case for ant species that have large foraging territories (*e.g.*, thatching ants (McIver and Yandell 1998) or carpenter ants (Sanders 1972)), in which the distances required to reach resource-rich patches necessitate efficient travel. Pitfall traps placed in close proximity or directly upon such a trail may accumulate a great number of individual ants, while an identical trap just a short distance away may sample few. Further, the capture of large numbers of individuals may

not be indicative of suitable resources in the immediate vicinity (few metres or tens of metres) of the pitfall trap as these individuals may simply be travelling through to a distant resource. For example, in our study, thatching ants, *F. obscuripes*, were captured more than 100 m from the nearest identified nest.

The patchy distribution of *F. obscuripes* around the five nests studied here suggest that the movement of workers is unique to each nest (Fig. 3) as would be expected for an ant focusing on the specific resources available within its foraging territory. In a Finnish study (Savolainen and Vepsäläinen 1989), two pitfall traps placed 5 m apart captured 30 and 1813 individuals of the boreal ant, *Formica polyctena* Foerster, at a distance of 10 m from their nest, and nine and 564 individuals at a distance of 60 m. This is consistent with the distribution in our study of *F. obscuripes*, which is ecologically similar to *F. polyctena*. In one instance, one pitfall trap collected 13 ants, as compared to 120 individuals in another pitfall trap just 10 m distant (Fig. 3, Nest 3). Traps surrounding one active colony (Fig. 3, Nest 2) yielded only a single individual throughout the entire 40 × 40 m grid sampled by 24 pitfall traps. The likely explanation is that this colony had well-established trunk trails leading out of the study grid and that the pitfall traps had not intercepted any of these.

Some authors have attempted to resolve the problem of highly variable captures of individuals by mathematically transforming the abundance capture data. This has included using a square root (Vanderwoude *et al.* 1997; Hamburg *et al.* 2004) or natural logarithm transformation of the total individuals captured. Other solutions reported in the literature include taking the number of individuals of a given species in a pitfall trap and dividing them by the total number of individuals of all species in the same trap to determine a proportional occurrence per pitfall trap or by adjusting the raw abundance of individuals by multiplying them by the frequency of occurrence (Lindsey and Skinner 2001; Wang *et al.* 2001b). Although such transformations would reduce the extent of the problem, no biological rationale is provided to validate the specific transformations used.

Other authors, however, prefer to use frequency of occurrence data exclusively (Romero and Jaffe 1989; Osborn *et al.* 1999; Andersen *et al.* 2002;

Martelli *et al.* 2004), where each species is tallied only as present or absent in each pitfall trap. This is a more cautious approach to interpreting pitfall trap data that gives consideration to the natural history of ants. It is supported by the distribution of *F. obscuripes* reported here.

Relating foraging ants to colonies: relative and absolute abundance estimates of ant assemblage structure

Absolute abundances are defined as population counts that arise from sampling a landscape or specific habitat per unit area or volume while relative abundances refer to sampling data that cannot be translated into taxon density estimates (Southwood and Henderson 2000). In the case of small invertebrates such as ants, only small areas can be effectively sampled for absolute abundance because of difficulties in locating nests, especially small cryptic nests (Anderson 1997) unless the nesting characteristics allow for focused searching (*e.g.*, species that nest in woody debris). This is unfortunate, as noted previously, because counts of ant colonies represent the most appropriate metric for assessing presence or absence given the theoretical consideration of the ant colony as a super-organism (Hölldobler and Wilson 2009) and the observation that the apparent abundance of foraging ants varies greatly with weather, time of day, and season. Pragmatic requirements, though, default to sampling techniques that are designed to concentrate on foraging ants. As a consequence, the issue that needs to be identified is the relationship between the apparent assemblage structure derived from relative abundance sampling and the less biased, at least in the context of ant colonies, estimates of absolute assemblage structure. In this study, we chose a grassland ecosystem to compare the apparent assemblage structure arising from these two sampling methodologies as this structurally simple ecosystem allows for accurate hand sampling of small areas.

Most notable was the observation that of the six species encountered, *L. crypticus* was the most common ant colony in the context of absolute abundance, but was much less common when considered in the context of relative abundance (*i.e.*, pitfall traps) (Fig. 4). This is likely because this species is reported to normally tend root aphids or mealybugs for honeydew (Wheeler and Wheeler 1963; Wheeler and Wheeler 1986) and is

likely less epigeaic than other species. *Tapinoma sessile* was the most relatively abundant species as determined from pitfall trapping, but less in absolute abundance (Fig. 4), although not significantly. This species is an active epigeaic forager that recruits quickly to food resources, a characteristic that makes them a common and efficient house pest (Wheeler and Wheeler 1963). As pitfall trap catches are a function of both abundance and the relative activity of epigeaic organisms, the high capture rates of *T. sessile* are to be expected. In addition, the absolute abundance of *M. crassirugis* also differed significantly from relative abundance as determined through tallying pitfall captures by presence–absence (Fig. 4). Finally, it is notable that the absolute abundance of *F. obscuripes* was zero despite these ants being recovered in pitfall traps, in two cases more than 100 m from the closest nest. In our study area, *F. obscuripes* nests were spatially scattered at distances frequently >100 m and were unlikely to be included in the small plots used for this study. This observation, however, illustrates a basic limitation of absolute abundance sampling in that intensive hand sampling is necessarily limited spatially and may miss large ant colonies that forage over large areas.

Conclusion

The Nordlander pitfall trap was shown to be equally efficacious to the conventional Laurent pitfall trap in sampling species richness while reducing the risk of vertebrate bycatch and offering some practical advantages in field placement. These pitfall traps were marginally superior to mini-Winkler litter sampling in developing estimates of total species richness in the cool-moist, subboreal forests of British Columbia, although some of that advantage may arise from a long period (2 weeks) of pitfall trap placement in this study. The relationship between the capture of foraging ants in pitfall traps and their natal colonies is complex and not related to the number of individual ants in a pitfall. Only presence/absence data should be used when considering pitfall trap captures and it should be recognised that ant assemblage structure arising from these data is still distinct from the absolute assemblage structure that would be developed from an assessment of colonies in a given area.

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