



Quantifying ant diversity and community in a subalpine forest mosaic: a comparison of two methods

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Abstract

Sampling efficiency, composition and detection biases associated with pitfall-trap and sample plot (standardised hand-collecting) methods were compared at seven high montane sites at Lasha Mountain, Yunnan, China. Rarefaction-interpolation curves showed total species diversity and sample coverage from each method were undifferentiated. Permutational multivariate analysis of variance showed highly overlapping communities. However, of all species collected, just 53% of all species found were shared between the two methods; 30% were exclusive to sample plot samples and 17% were exclusive to pitfall traps. Modelled comparisons of species richness (alpha) and proportion of species from the population (beta diversity) showed differences between methods. Permutational multivariate analysis of variance blocked by site showed community composition differed between methods, defined largely by the presence of a few dominant species.

Implications for insect conservation: Our findings suggest that results from the two methods cannot be directly compared and are imperfect substitutes to one another. For long-term monitoring of biodiversity in complex forest mosaic systems, we suggest integrating a suite of complementary methods to achieve more complete representation of ant composition and diversity.

Keywords Ant survey · Sampling method · ground-dwelling, epigeaic · Hypogaeic · Formicidae · Hengduan Mountains · Eastern Himalaya

Introduction

Global biodiversity is declining at an unprecedented rate (IPBES 2019). Monitoring biodiversity is a key part of addressing the trend by providing facts of the occurring

changes and mechanisms of change to bring about science-based policy and land management decisions that benefit biodiversity (Noss 1990; Hobbie et al. 2003; Kuussaari et al. 2009; Cardoso et al. 2011; Navarro et al. 2017; Guerra et al. 2021). The continuing challenge is measuring

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biodiversity in ways that are useful, accurate, and repeatable (Purvis and Hector 2000; Lindenmayer and Likens 2010). Ants, in particular, are an insect group of immense ecological significance, contributing a large proportion of the global arthropod biomass (Schultheiss et al. 2022) and having critical ecological functions such as nutrient cycling, soil aeration, and seed dispersal (de Bruyn and Conacher 1990; Hölldobler and Wilson 1990; Folgarait 1998; Parr et al. 2016; Penn and Crist 2018). Ants are relatively easy to collect, sensitive to environmental change and representative of soil diversity (Andersen et al. 2004; Andersen and Majer 2004; Li et al. 2015a). As such, ants have long been an important insect group for biological monitoring and indicators of ecological change (bioindicators) (Andersen 1997; McGeoch and Chown 1998; Andersen et al. 2002; Underwood and Fisher 2006; Zhang and Ou 2006; Gerlach et al. 2013; Tiede et al. 2017).

Several sampling methods have been developed to collect ants, each with their own strengths and weaknesses (Bestelmeyer et al. 2000). Understanding the limitations to sampling techniques is important to selecting a method, or combinations of methods, that will address survey objectives within a given environment, sampling effort and available expertise (Bestelmeyer et al. 2000; Gotelli et al. 2011; de Souza et al. 2012). To allow stricter comparison of individual studies, numerous researchers have advocated for the adoption of recognised standard protocols (e.g., Li et al. 2009; Antoniazzi et al. 2020). Such protocols have been proposed (e.g., Ants of the Leaf Litter (ALL) Protocol: Agosti and Alonso 2000) and successfully applied (Vineesh et al. 2007; Lopes and Vasconcelos 2008; Bray 2014; Yeo et al. 2017) but universal application has lagged.

In China, the ‘sample-plot’ (样地调查法) is a common method for sampling ants (Xu et al. 1999), followed by pitfall traps. Pitfall traps are small, covered pits set in the ground that target active epigeic (ground-active) fauna (Bestelmeyer et al. 2000). The widely used method provides relatively simple and cost-effective sampling that allows for continuous day and night sampling (Majer 1997). However, pitfall traps suffer for their sensitivity to species size, activity, and susceptibility (Marsh 1984; Topping and Sunderland 1992; Majer 1997) as well as biases to do with trap diameter, trap depth, spacing and habitat complexity (Luff 1975; Adis 1979; Majer 1997; Ward et al. 2001; Jiménez-Carmona et al. 2020). The sample plot method—a modified ‘direct sampling’ method (Bestelmeyer et al. 2000)—is a technique where specimens are collected systematically from microhabitats using a range of hand-collecting techniques within a specified area and time (Xu 2002). The method has advantages in efficiency but is vulnerable to the competence of the researchers and differences in habitats,

reducing the comparability between samples and studies (Bestelmeyer et al. 2000).

Here, we aimed to evaluate these two widely used sample methods in China for long-term ant biodiversity monitoring by assessing their results in terms of ant diversity and community composition in a forest mosaic in Yunling Nature Reserve, Yunnan Province. We expected that sample plot methods would collect more ant species than pitfall traps, where hand sorting could allow for sampling of more cryptic, less abundant and slow-moving ants (Parr and Chown 2001; Longino et al. 2002; de Souza et al. 2012; Mark and Guenard 2017). We also expected that sampling methods may selectively filter the ant community present so that combining methods could improve the survey and generate a closer estimation of true ant community (Longino and Colwell 1997). Our results will provide a measure of the sampling effort required and reliability of the combination of methods to characterise and monitor ground-dwelling ant diversity in a high montane forest mosaic.

Materials and methods

Study area

The study was conducted at Lasha Mountain (拉沙山) (N26°20′, E99°15′) in Yunling Nature Reserve, Yunnan, China, within the Mountain Area of Southwest China biodiversity hotspot (Myers et al. 2000). At 75,894 km², the Yunling Nature Reserve comprises a mosaic of land covers, including subalpine forest, regenerating forest, pastoral grazing land, cropland, and permanent settlements. The study area is a ca. 1400 ha catchment ranging from 2500 to 3700 m asl. Forest vegetation dominates most of the mid-elevations, transitioning from deciduous broadleaved forest (*Betula alnoides*, *Acanthopanax gracilistylus*, *Acer oliverianum*) at lower elevations, through mixed deciduous-conifer forest to conifer forest (*Abies georgei*, *A. fabri*, *Tsuga dumosa*) at the highest elevations. The forest undergrowth primarily comprises *Rhododendron* spp. and bamboo (*Fargesia strigosa*, *F. edulis*, *F. solida*). Few local families live in the lowest part of the catchment where there is a mixture of grazing, cropland and forest margins. The forest is used by local people for resources such as wood, traditional foods and medicine (Huang et al. 2017). The climate is characterised by alternating dry (winter) and wet (summer) seasons, with an annual mean precipitation of 910 mm (Wang et al. 2012; Li et al. 2019).

Sample design

We sampled ants using two common sampling methods (pitfall trap and sample plot) across the study area. For every 200 m elevation from 2500 to 3700 m, we established one 60 m × 60 m sample site (totalling 7 sites) using the stream as a centreline. Seven pitfall traps were stratified across each site. The open-topped attractant bottles (11 cm in diameter, 15.5 cm in height) were embedded into the ground until flush with the natural soil surface and covered with 15-cm diameter plastic plates to keep rain out. Traps were baited with 50–70 ml liquid attractant composed of 1:1:4:16 solution of ethanol, sugar, vinegar, water (Chen et al. 2011; Li et al. 2017; Fang and Xu 2021). Trap surveys were conducted from August to September in 2018, 2019 and 2020. For each year, traps were shifted to new locations within the sample site for the duration of that year. We emptied traps every two weeks during each sampling period.

Sample plot sampling was undertaken at five 5 m × 5 m sampling plots stratified across each site. After an initial surface inspection, ants were collected by hand from litter, decaying wood and under stones for 24 min (one person) using forceps and aspirators. Using hand tools, soil was excavated to 20 cm to search for and collect ants from subterranean nests. A maximum thirty individuals were collected from a single nest. Foliage collections were made using a 2 m × 2 m white curtain was placed flat around the sample plot and small trees and shrubs up to 5 m were vigorously shaken or beaten to capture ants that fell on the curtain. In total, each 5 m × 5 m plot required approximately 0.5 h to complete, including 24 min of investigation and the time required to return litter, soil or up-turned logs to their original position. Sample plot surveys were completed once for each site in August 2017.

Collected specimens from both methods were stored in 75% ethanol and transferred to a freezer at -10 °C before being identified (Xu 2002).

Statistical analysis

All analyses were performed using R v4.2.0 (R Core Team 2020). Sampling yielded 28 sampling units in total from 21 pitfall trap units and 7 sample plot units. We considered a species × samples matrix with presence-absence data (30 species × 28 samples for all species together).

To visualise the number of species of ants detected with each method, a Venn diagram was drawn using the ‘eulerr’ package in R (Larsson 2021). We drew these for all species, as well as species classed as “dominant”, “common”, and “rare.” We defined dominant species as those with a total relative abundance exceeding 10%; common species contributed between 1% and 10% total abundance, and rare

species contributed less than 1% to the total population sampled (Li et al. 2015a).

The effects of method on total measured alpha (α) and beta (β) diversity were tested using a Linear Mixed-Effects Model, using the function `lmer` in the ‘lme4’ package in R (Bates et al. 2015) with parametric analysis of variance (ANOVA). ‘Site’ was introduced as a random effect in the model. Normality and homogeneity of variance were checked by performing Quartile-Quartile (QQ) plots of the residuals and fitted models using the function `plotresid` in the package ‘RVAideMemoire’ (Hervé 2018). We identified and removed outliers in the model using the function `romr.fnc` in the package ‘LMERConvenienceFunctions’ (Tremblay and Ransijn 2015).

We used rarefaction analysis to compare estimated asymptotic species diversity between the sample plot and pitfall trapping methods, a technique based on species frequency (i.e., presence-absence) that avoids biases caused by insufficient or differing sampling efforts (Gotelli and Colwell 2001). To do this, we used sample-sized-based rarefaction-extrapolation analysis based on sampling-unit-based incidence data for each sampling year (Chao et al. 2014a, b). Hill species diversity (or the effective number of species) in the zero ($q=0$), first ($q=1$), and second ($q=2$) orders (or species richness, the exponential Shannon entropy, and inverse Simpson index, respectively) were computed in the ‘iNEXT’ package (Hsieh et al. 2016). In addition, we compared sampling coverage (based on incidence) of each method across Hill species diversities to our sampling effort, permitting estimation of the proportion of the total community represented by the sampling effort and an assessment of sample completeness (sample coverage) across sampling units (Chao and Jost 2012; Chao et al. 2014a; Hsieh et al. 2016). Significant differences in estimated diversity and sampling coverage between methods were judged by non-overlapping confidence intervals (Chao et al. 2014a, b).

To evaluate differences in ant composition of samples obtained from the two methods, we performed non-metric multidimensional scaling (NMDS: calculated with Jaccard dissimilarity index) with the function `metaMDS` of the R package ‘vegan’ (Oksanen et al. 2019). We considered a species × sample matrix with presence-absence data (30 species × 28 samples). We used presence absence data to avoid assumptions of independence of individual workers (Longino et al. 2002). A dummy species was added to the species matrix to mitigate the impact of pitfall traps that had zero abundances (Clarke et al. 2006). To test for differences between groups (methods), we used a permutational multivariate analysis of variance (PERMANOVA) using distance matrices, which was performed with the function `adonis2` in `vegan` (Oksanen et al. 2019). Because we anticipated assemblages might vary across sites, we conducted the analysis

both without and with site as a grouping factor. P values were obtained using 9999 permutations of residuals. To determine which species contributed most to the observed multivariate differences between pitfall trapping and sample plot methods, we used similarity percentage analysis (SIMPER) (Clarke 1993).

Results

Ant collection

Using two sampling methods, we found a total of 10,206 ant (Insecta: Formicidae) specimens belonging to four subfamilies (Myrmicinae, Formicinae, Dolichoderinae, and

Ponerinae), 17 genera and 30 species (Table 1; SI 1). Of these, 6312 and 3894 individuals were collected from pitfall trap and sample plot methods respectively. We recorded, 21 species from pitfall traps and 25 species from sample plots, of which only 16 species (53%) were shared (Fig. 1). The most abundant ('dominant') species across sampling methods were *Pheidole nietneri* Emery, 1901, *Myrmica rugosa* Mayr, 1865, *Myrmica kozlovi* Ruzsky, 1915, *Myrmica bactriana* Ruzsky, 1915, *Formica fusca* Linnaeus, 1758, together accounting for 70% of all the specimens collected (Table 1; Fig. 1). We recorded 11 rare species from pitfall traps and 14 rare species from sample plots, seven of which were shared. Rare species contributed 5% to the total specimen abundance. All species were within their known natural distributions.

Table 1 Number and account of species in Sample-plot method and Pitfall-trap method. For Classes, D=dominant species (>10% of total); C=common species (1–10% of total); R=rare species (<1% of total); (%) = % contribution to total abundance

| Subfamily/species | Class | Pitfall Trap | Sample Plot | Sum | (%) |
|--|-------|--------------|-------------|---------------|------|
| Dolichoderinae | | | | | |
| <i>Tapinoma sinense</i> Emery, 1925 | C | 0 | 106 | 106 | 1.04 |
| Ponerinae | | | | | |
| <i>Ponera bawana</i> Xu 2001 | R | 1 | 0 | 1 | 0.01 |
| Myrmicinae | | | | | |
| <i>Aphaenogaster caeciliae</i> Viehmeyer, 1922 | C | 100 | 119 | 219 | 2.2 |
| <i>Aphaenogaster lepida</i> Wheeler, 1930 | R | 0 | 3 | 3 | 0.03 |
| <i>Myrmica bactriana</i> Ruzsky, 1915 | D | 490 | 697 | 1187 | 11.6 |
| <i>Myrmica jessensis</i> Forel, 1901 | R | 0 | 1 | 1 | 0.01 |
| <i>Myrmica kozlovi</i> Ruzsky, 1915 | D | 257 | 988 | 1245 | 12.2 |
| <i>Myrmica margaritae</i> Emery, 1889 | R | 35 | 2 | 37 | 0.4 |
| <i>Myrmica pararitae</i> Radchenko, 2008 | R | 1 | 98 | 99 | 1.0 |
| <i>Myrmica ritae</i> Emery, 1889 | R | 38 | 26 | 64 | 0.6 |
| <i>Myrmica rugosa</i> Mayr, 1865 | D | 1344 | 207 | 1551 | 15.2 |
| <i>Myrmecina striata</i> Emery, 1889 | R | 3 | 0 | 3 | 0.03 |
| <i>Pheidole nietneri</i> Emery, 1901 | D | 1955 | 2 | 1957 | 19.2 |
| <i>Pheidole pieli</i> Santschi, 1925 | R | 0 | 1 | 1 | 0.01 |
| <i>Perissomyrmex bidentatus</i> Zhou & Huang, 2006 | R | 0 | 8 | 8 | 0.08 |
| <i>Temnothorax</i> sp.1 | R | 1 | 10 | 11 | 0.1 |
| <i>Temnothorax</i> sp.2 | R | 1 | 0 | 1 | 0.01 |
| <i>Tetramorium kraepelini</i> Forel, 1905 | R | 43 | 5 | 48 | 0.5 |
| <i>Stenamma bhutanense</i> Baroni Urbani, 1977 | R | 1 | 49 | 50 | 0.5 |
| Formicinae | | | | | |
| <i>Camponotus anningensis</i> Wu & Wang, 1989 | R | 0 | 52 | 52 | 0.5 |
| <i>Camponotus herculeanus</i> Linnaeus, 1758 | C | 19 | 90 | 109 | 1.1 |
| <i>Lasius flavus</i> Fabricius, 1782 | R | 0 | 2 | 2 | 0.02 |
| <i>Lasius coloratus</i> Santschi, 1937 | R | 9 | 39 | 48 | 0.5 |
| <i>Lasius alienus</i> Foerster, 1850 | C | 686 | 273 | 959 | 9.4 |
| <i>Nylanderia bourbonica</i> Forel, 1886 | R | 0 | 2 | 2 | 0.02 |
| <i>Nylanderia flavipes</i> Smith, 1874 | C | 53 | 96 | 149 | 1.5 |
| <i>Paraparatrechina aseta</i> Forel, 1902 | C | 0 | 202 | 202 | 2.0 |
| <i>Prenolepis angularis</i> Zhou, 2001 | R | 70 | 0 | 70 | 0.7 |
| <i>Formica fusca</i> Linnaeus, 1758 | D | 360 | 816 | 1176 | 11.5 |
| <i>Formica sinensis</i> Wheeler, 1913 | C | 844 | 0 | 844 | 8.3 |
| Total | | 6312 | 3894 | 10,206 | |

Fig. 1 Numbers of unique and common ant species for pitfall trap (PF) and sample plot (SP) samples are depicted in a Venn diagram for All, ‘Dominant’, ‘Common’, and ‘Rare’ species

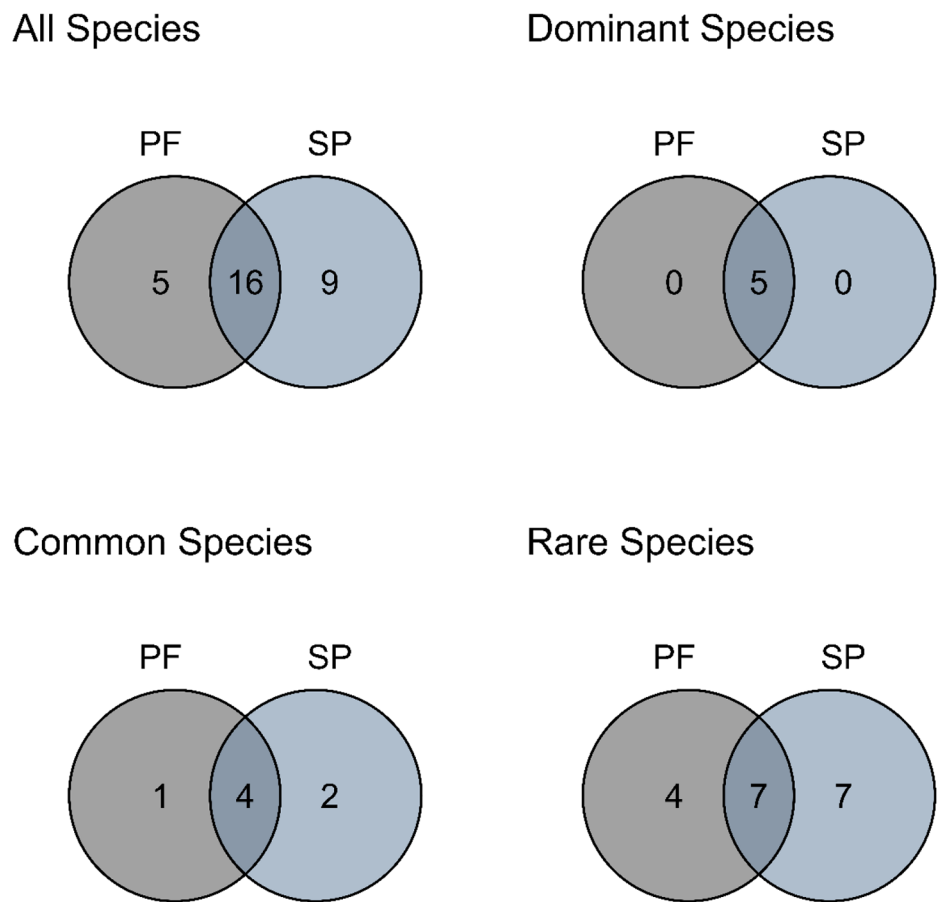
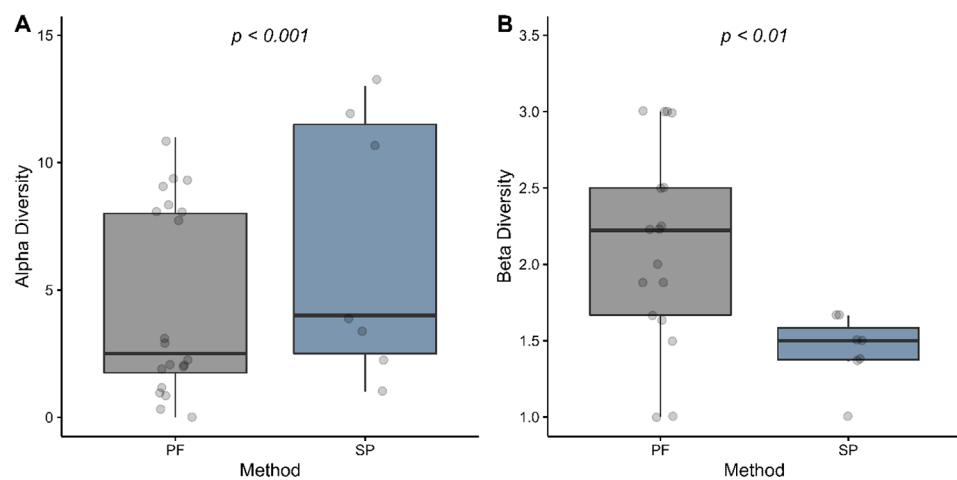


Fig. 2 Effect of method to total alpha (species richness) and beta diversity. PF: pitfall trap; SP: sample plot



Species diversity

Comparisons of observed ant species richness, with ‘site’ as a random factor, showed the sample plot method had higher measured alpha diversity than the pitfall trapping method (Fig. 2; SI 2). The sample plot method also had significantly higher proportion of site-level diversity in samples (beta diversity) in comparison to the pitfall trapping method with

the same model (Fig. 2; SI 2). However, rarefaction-extrapolation curves based on inter-annual collections showed ant species diversity across all sites were undifferentiated (overlapping confidence intervals) for sampling method for all three estimators of diversity (Fig. 3). Total estimated species richness was 35 ± 7.7 s.e. for sample plot method; for pitfall traps, total estimated species richness was 23 ± 7.7 s.e. in 2018, 26 ± 7.3 in 2019, and 24 ± 7.8 s.e. in 2020 (SI 3).

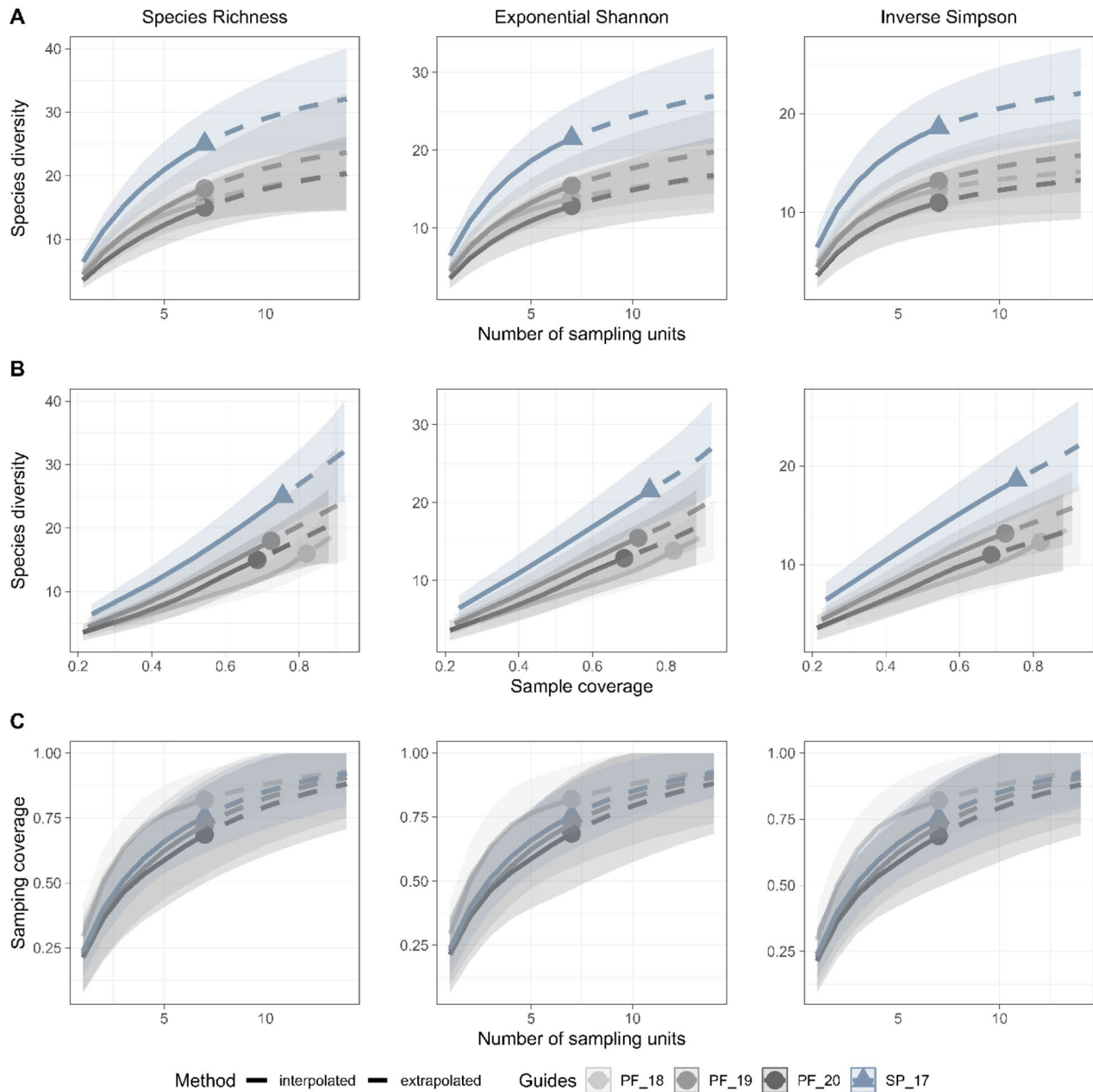


Fig. 3 Sample-based rarefaction (solid lines) and extrapolation (dotted lines) of ants collected using pitfall trap (PF) and sample-plot (SP) methods, with 95% unconditional confidence intervals (shading). Diversity was estimated for species richness, exponential Shannon's index, and inverse Simpson's index. (A) A comparison of estimated

asymptotic or true diversities for two methods (PF and SP); (B) a comparison of estimated point diversities for sampling units for methods PF and SP; (C) an assessment of sample completeness (sample coverage) across increasing sample units

Rarefaction results were consistent when comparing diversity at a given sampling effort and coverage (Fig. 3B–C). The sampling coverage completeness for species richness was 76% for the sample plot method, and 82%, 72% and 69% for the pitfall trap method in each year, respectively. To achieve more than 95% sample coverage sample size would need to be increased more than three-times (SI 4).

Community composition

The NMDS plots based on species presence-absence without blocking showed highly overlapping communities (SI 5), whereas NMDS plots showed some clustering according to method when blocked by site (Fig. 4). Accordingly, PERMANOVA results PF and SP assemblages were undifferentiated without blocking, whereas PF and SP assemblages

differed significantly when blocked by site ($p < 0.05$). The NMDS analysis had a low stress value (0.07) which indicates that the ordination summarised the observed distances between samples well (Fig. 4). The SIMPER analysis showed that *Myrmica kozlovi*, *M. baccirana*, *M. rugosa* and *Formica fusca* contributed the most to the difference in communities between sample methods, collectively contributing 31% to total between method community variation (SI 6). Exclusive species contributed 25% to between method dissimilarity.

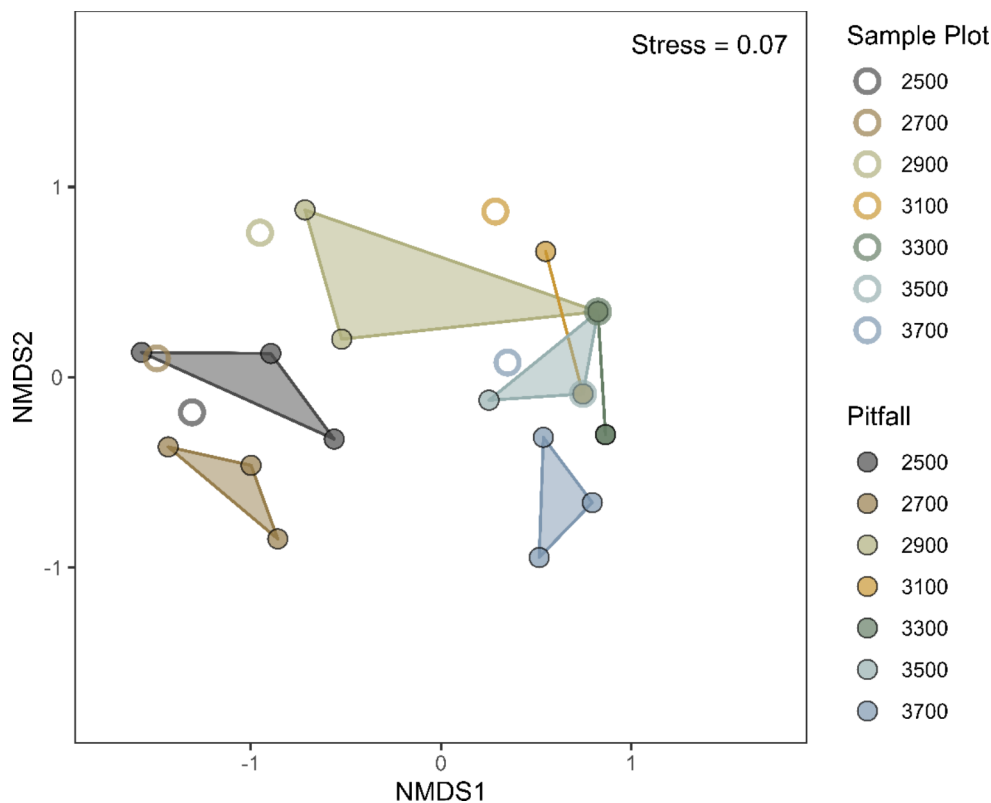
Discussion

Our expectation was that sample plot methods would collect more species and accumulation curves would be steeper than those from pitfall traps (Ellison et al. 2007; Abril and Gómez 2013). Our assumption was hand sorting would better target small and slow-moving ants, as well as ants from specific micro-habitats (Andersen 1991; Longino et al. 2002; Véle et al. 2009; Gotelli et al. 2011; de Souza et al. 2012; Mark and Guenard 2017). Instead, comparisons of the efficiency of species accumulation using rarefaction analysis showed interpolated and extrapolated diversity metrics were undifferentiated. Both methods were effective at collecting the most common species across sites, and permutational multivariate analysis across site community assemblages were largely overlapped. However, when we applied ‘site’

as a random factor to our models, differences of alpha and beta diversity and community structure became apparent. At a given site, sample plot methods generally measured a greater species richness, and consequently pitfall traps tended to sample a smaller proportion of the total diversity. Community structure, driven by the relative presences (or absences) of a few dominant and wide-spread forest litter species, differed between methods within sites according to permutational multivariate analysis, suggesting the variation between sites was greater than the variation between methods.

Both methods recovered species undetected by the other method. We found 14 of 30 species were exclusive to one method, representing a range of size-classes, foraging strategies, and nesting behaviours. Contrary to our assumption that pitfall traps would bias large species (Abensperg-Traun and Steven 1995), the proportion of small (2–4 mm) species exclusively collected by each method were comparable, with large (> 5 mm) species represented by *Formica sinensis* in pitfall collections, and *Aphaenogaster lepida* and *Camponotus anningensis* in sample plot collections. In addition, we expected the sample plot method would detect more species that seldom occur above ground, exhibit cryptic feeding behaviour, or occupy small (1–2 m) foraging ranges (Sanders et al. 2007; Véle et al. 2009). Of the exclusive species, only two species exhibiting these traits were observed, one by each method: *Ponera bawana*, a cryptobiotic foraging species nesting in rotting logs or under stones, was collected

Fig. 4 An NMDS ordination plot indicating the congruence in ground-dwelling ant species associations among sites (2500–3700) and sampling techniques (pitfall trapping and sample plot) at Lasha Mountain, Yunnan, China. Lines connect pitfall trap samples from a common site



in pitfall traps (Taylor 1967; Xu 2001); and *Lasius flavus*, a hypogaecic (soil-dwelling) species that nests in the soil and under stones and is only rarely observed above ground (Wilson 1955), was detected by hand collection using the sample plot method.

Of exclusive species, we judged 11 to be rare (contributing less than 1% to the total sample). Rare species comprise a high proportion of most highly diverse communities (Novotný and Basset 2000; Burner et al. 2022b) and are important indicators of environmental change (Dopheide et al. 2020). Rare species are also highly sensitive to sampling effort and stochasticity in the environment (Novotný and Basset 2000; Burner et al. 2022a), so that inflating the importance of species appearing in only one sampling method could be misleading. In this study, we estimated sampling effort would need to be doubled to approach 90% sampling coverage of estimated site diversity, and over three times to reach 98% sampling coverage estimated site diversity. With increased sampling or replaying chance encounters, we contend unique (and typically rare) species captured with one sampling method could have also been captured by the other method (Gotelli et al. 2011; Antoniazzi et al. 2020).

A goal of ecological monitoring is comparing year-on-year population or community-level changes (Longino and Colwell 1997; Underwood and Fisher 2006; Lindenmayer and Likens 2010). Comparisons might be to track relative responses to environmental change (e.g., Edwards et al. 2012), or track species interactions (e.g., Sanders et al. 2001; Morgan Ernest et al. 2016). The variety of sampling methods and nuanced protocols add complications when we want to compare results. Long-term monitoring is best accomplished with methods that are, particularly in remote and under-developed regions, simple and cheap, but importantly they need to be robust, repeatable, and comparable. The challenge is that no single method will provide a comprehensive sampling, and each method has its own limitations and biases. For example, Winkler extractions have often been shown to be one of the most effective methods for sampling ants forested ecosystems with substantial litter (e.g., Fisher 1999; Bestelmeyer et al. 2000; Delabie et al. 2000; Martelli et al. 2004; Lessard et al. 2007; Ivanov and Keiper 2009; Ivanov et al. 2009; Sabu et al. 2011); however, subalpine forests, driven by extreme environmental gradients and impacted by centuries of human habitation, often form discontinuous canopies and marginal litter base than more temperate forests. Mature forests are often isolated by non-forested grazing land and intermediate seral communities. Collecting soil monoliths (or turves) offers a robust spatially quantitative method for monitoring soil fauna that is successful across environments (Potapov et al. 2022); samples can be either hand-sorted or extracted using a Berlese-Tullgren funnels (Véle et al. 2009; Yeo et

al. 2011; Martins et al. 2020; Basset et al. 2022). Drawbacks are monoliths can be difficult to process in the field, are heavy to transport, and may impact sites long term. Berlese-Tullgren funnels offers a solution to hand-processing (e.g., Barratt et al. 2005; Barratt et al. 2009; Basset et al. 2022) but requires specialised (or purposed-built) equipment, an issue also with using Winkler extractions.

Pitfall traps are cheap, easy to install, and the materials are easily available even in rural China. They are particularly effective in open, less structurally complex vegetation such as grassland, heathland, alpine and savanna ecosystems (Parr and Chown 2001; Steiner et al. 2005; Oliveira et al. 2009; Spotti et al. 2015; Hoffmann and Pettit 2022). It is important to recognise that traps are spatially constrained (Luff 1975; Majer 1997), traps bias active, large-bodied epigaecic species (Abensperg-Traun and Steven 1995), and counts of ants in traps are not independent to one another (Gotelli et al. 2011). Species may vary in their susceptibility to trapping capture, where some species may be more attracted to traps, whereas some species may actively avoid traps (Marsh 1984). The number and composition of ants collected may also be influenced by collection solution (Calixto et al. 2007) or bias resource dominant species where traps are baited (Gotelli et al. 2011). While un-baited traps should improve comparability between studies, we reduced the influence of individual traps by bulking multiple traps.

Active searches, or hand collecting, is an efficient method for recording ant diversity (Andersen 1991; Bestelmeyer et al. 2000; Sanders et al. 2001; Longino et al. 2002; Ellison et al. 2007; Abril and Gómez 2013; Fotso Kuate et al. 2015; Antoniazzi et al. 2020; Massé et al. 2021). Its popularity among scientists is likely stifled because conformity in search time and area protocols are still lacking consensus and concerns for variability in expertise pervade (Gotelli et al. 2011). The sample-plot method is one active species-collection method that employs a standardised set of hand-sampling techniques (i.e., quadrat sampling (Bestelmeyer et al. 2000), nest excavation (Romero and Jaffe 1989), and foliage beating (Harris et al. 1972). It targets available microhabitats—decaying woody material, litter, surface soil and foliage—within a defined space and time (Xu 2002). On a sampling unit basis, we found the combined relative field and laboratory time efficiencies of the sample plot and pitfall trapping methods were comparably similar. One advantage of the sampling plot method we experienced was that field collections were completed in a single site visit, which can be advantageous where sites are remote. Limitations are the sample plot surveys can only be conducted in the daytime (i.e., adequate lighting) and in fair weather (Li et al. 2015b), and hand searches may not be efficient where ants are cryptic or primarily nocturnal. We also found habitats with densely vegetation and abundant coarse woody

material were difficult and may (given the time constraint) have been under-sampled in comparison to less complex habitats.

One commonly referred impediment to widespread use of hand collecting is the concern to repeatability between observers. Expert collectors can accumulate species much faster than others and may unconsciously bias novel species by passing over common species (Longino et al. 2002; Sørensen et al. 2009; Gotelli et al. 2011; Antoniazzi et al. 2020). For this reason, Gotelli et al. (2011) suggests naive collectors may be more effective at accumulating species in relative proportion to their true colony densities. Regardless, dealing with the effect of individual collectors can be practically dealt with by adding “collector” as a random factor to models (Antoniazzi et al. 2020). In our study, sample plot samples were collected using students with direct guidance from a myrmecologist, so we are unable to verify the importance of expertise for completeness or consistency. For remote biological surveys, particularly in areas with prominent local or indigenous groups presence, such as Lasha Mountain, a test for the method will be if long-term biological monitoring can be facilitated by interested locals (Basset et al. 2004). Lasha Mountain has communities representing multiple ethnic nationalities that depend on the local biodiversity and the sustainable management of natural resources for their livelihoods. Establishing methods that can involve indigenous or local people, many of whom have indigenous knowledge, can benefit research as well as improve situations for local people (Braschler et al. 2010).

Another condition for effective long-term biological monitoring is that the methods need to be non-destructive with negligible impact to the local population and supporting habitat (Zaller et al. 2015). This is particularly important in small habitat fragments, sensitive sites, or where species of concern (e.g., ‘threatened’ species) exist (Samways et al. 2010). For example, a common concern of pitfall traps as a monitoring tool is the potential to reduce the overall abundance of invertebrate populations in the local area. Likewise, a strong argument against the use of the sample plot method as a monitoring tool is that repeated soil excavations, destructive searches and collector trampling may have lasting impacts to the micro-habitat, vegetation, and soil. For sample plots, we allowed time to ‘reconstruct’ each plot after intensively searching (turning over logs and rocks, sifting through litter) and excavating soil, although, we cannot be certain the future impacts. We suggest options to modify monitoring frequency or non-destructive alternatives (e.g., Bowie and Frampton 2004) need consideration.

In summary, our results showed both methods are effective for measuring and monitoring ant populations in forest systems. By some metrics, the methods were undifferentiated, but overall selected differently from ant populations.

Our conclusion is that the pitfall trap and sample plot methods are effective complements as part of an integrated survey with a low risk of redundancy (Tista and Fiedler 2011; de Souza et al. 2012), giving support to advocates of implementing a diversity of methods, where time labour and expense are not limited (e.g., Bestelmeyer et al. 2000; Basset et al. 2012; de Souza et al. 2012; Antoniazzi et al. 2020; Basset 2020), to improve survey sensitivity and accuracy.

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Declarations

Competing interests The authors declare no competing interests.

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