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Biodiversity below ground: probing the subterranean ant fauna of Amazonia

Kari T. Ryder Wilkie · Amy L. Mertl · James F. A. Traniello

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Abstract Ants are abundant, diverse, and ecologically dominant in tropical forests. Subterranean ants in particular are thought to have a significant environmental impact, although difficulties associated with collecting ants underground and examining their ecology and behavior have limited research. In this paper, we present the results of a study of subterranean ant diversity in Amazonian Ecuador that employs a novel probe to facilitate the discovery of species inhabiting the soil horizon. Forty-seven species of ants in 19 genera, including new and apparently rare species, were collected in probes. Approximately 19% of the species collected at different depths in the soil were unique to probe samples. Analysis of similarity (ANOSIM) results showed that the species composition of ants collected with the probe was significantly different from samples collected using other techniques. Additionally, ANOSIM computations indicated the species assemblage of ants collected 12.5 cm below the surface was significantly different from those found at 25, 37.5, and 50 cm. Ant diversity and species accumulation rates decreased with increasing depth. There were no species unique to the lowest depths, suggesting that subterranean ants may not be distributed deep in the soil in Amazonia due to the high water table. The technique we describe could be used to gain new insights into the distribution and biology of subterranean ant species and other members of the species-rich soil invertebrate macrofauna.

Keywords Soil fauna · Formicidae · Species richness · Conservation · ALL protocol

K. T. Ryder Wilkie (✉) · A. L. Mertl · J. F. A. Traniello
Department of Biology, Boston University,
5 Cummington Street,
Boston, MA 02215, USA
e-mail: karitr@bu.edu

Introduction

The exceptional abundance and diversity of ants underscores their importance to tropical ecosystems (Hölldobler and Wilson 1990; Folgarait 1998; Floren et al. 2002; Bolton et al. 2006). Indeed, ants serve the function of "soil engineers" and are necessary to ecosystem health (Lavelle et al. 1997; Folgarait 1998). Although the soil and ground litter of tropical angiosperm forests is considered the "headquarters of ant evolution" (Wilson and Holldobler 2005), subterranean ants are underrepresented in biotic surveys due to the difficulties of collecting underground. The significance of army ants as keystone species in some habitats, for example, is largely based on studies of *Eciton* and epigaeic species of *Dorylus* (Gotwald 1995; Boswell et al. 1998; Brown and Feener 1998; Kaspari and O'Donnell 2003). The majority of army ant genera, however, are hypogaeic. In addition, whole genera such as *Acropyga* appear to be entirely subterranean and form ecologically significant symbioses (Williams 1998).

It is widely believed that the diversity and abundance of subterranean ants may be greater than current surveys indicate (Longino and Colwell 1997). The subterranean ant fauna may in fact be the "final frontier" in the study of the biodiversity of the Formicidae. Attempts to inventory this elusive fauna have included baiting (MacKay and Vinson 1989; Yamaguchi and Hasegawa 1996; Fowler et al. 2000; Weissflog et al. 2000; Berghoff et al. 2003a, b) and soil-core sampling (Delabie and Fowler 1995; Longino and Colwell 1997; Lindsey and Skinner 2001; Fisher and Robertson 2002). These methods are often time-consuming, labor intensive, intrusive, and thus limited in their ability to accurately assess the spatial and temporal structure of the hypogaeic ant community. In this paper, we describe a new device that facilitates discovering and studying ants in the soil horizon and present results of research on subterranean ant diversity in Amazonian Ecuador, comparing the effectiveness of our belowground sampling technique with traditional collecting methods. We analyze patterns of ant species richness in different strata to determine the similarity of the subterranean fauna with other ant assemblages.

Materials and methods

We used baited cylindrical probes to collect ants at different soil depths in primary *terra firme* rainforest at the Tiputini Biodiversity Station (TBS) in Amazonian Ecuador during July–August of 2004. TBS (00°37′05″S, 76°10′19″W) is located in Orellana Province, Ecuador, and is adjacent to Yasuni National Park, which is widely considered to be one of the world's most diverse hotspots. In 1989, it was designated as a UNESCO Biosphere Reserve, in recognition of its extraordinary biodiversity. No comprehensive inventory of ants at TBS has yet been published, but previous studies (Kaspari et al. 2000a, b) at Yasuni indicate diversity is high in the area.

Ten probes, each separated by 20 m (total = 50 probe station samples), were implanted along each of five 200-m transects separated by 200 m. The probe consisted of two 50-cm-long plastic cylinders made from polycarbonate tubing. One cylinder (outer diameter = 2.0 cm; inner diameter = 1.5 cm) was implanted in the ground after a hole of the same diameter and length was drilled in the soil using a portable power drill (DeWalt 2.5 in/6.35 cm 24 V cordless hammerdrill and 24 in/61 cm auger). This outer cylinder received a second removable cylinder (inner diameter = 1.0 cm; outer diameter = 1.5 cm) precisely fitted to its interior (Fig. 1). The inner probe could thus be removed and replaced to allow repeated monitoring without disturbing the surrounding soil. Both cylinders were perforated, allowing ants to occupy baits (protein and carbohydrate) in each of four compartments at depths of 12.5, 25, 37.5, and 50 cm below the surface. The perforations in the inner and outer cylinders were aligned by a notch in the top of the outer cylinder. Each bait compartment was physically separated and threaded to allow ants in adjacent compartments to be removed. Ants in one compartment could not move within the probe to another compartment. Therefore, the location of ants within the probe indicated the depth at which they search for food and/or nest. The soil surface surrounding an implanted probe was covered by plastic sheeting (approximately 1 m^2) pegged tightly to the ground to minimize water accumulation in the device. Probes were censused 24, 48, and 72 h after placement. Information on the construction of our subterranean probe can be found online at http://people.bu.edu/jftlab/DIYprobe.html.

All ants collected in probes were identified to species or morphospecies and were compared with type specimens in the ant collection of the Harvard Museum of Comparative Zoology or sent to experts for identification.

To examine the uniqueness of ants in the subterranean samples, we compared the distribution of ants found in probes (N=50) with ants collected by traditional sampling methods [Winkler and pitfall traps, surface baits, and hand collecting (N=60 samples each along three of the five transects) and canopy fogging (N=78 samples along ten transects, including the five transects from this study)]. In total, we collected ~113,000 ants using all techniques. To date, we have identified 436 species/morphospecies in 64 genera from all samples, with ~96% of species identifications completed. We estimate local species richness to be ~500 species (Ryder Wilkie et al., unpublished data). Traditional sampling methods were carried out by Ryder Wilkie during February and March of 2003, following the methodology described in Agosti et al. (2000). Canopy foggings were carried out by Erwin between 1994 and 2002 according to the methods described in Erwin (1989).

EstimateS (version 8.0; Colwell 2005) was used to generate species accumulation curves (Sobs, Mau Tau), which were fit to a logarithmic model. Analyses of similarity (ANOSIM; Clarke 1993) comparisons were performed using the one-way ANOSIM function in the PAST software package (version 1.57; Hammer et al. 2001) to detect differences between the diversity of ants in probe samples and other collection methods. In these analyses, data on the diversity of ant genera were used to compare assemblage similarity and estimated similarity because species identifications of all nonprobe ants are still pending. The analysis reported here thus provides a conservative measure of similarity. All genera collected using all collection methods were used in this analysis. One-way ANOSIM comparisons were also carried out to detect differences between species assemblages collected at different probe depths. These analyses involved only those species collected in probes. All ANOSIM calculations used the Jaccard similarity coefficient calculated from presence–absence data with 5,000 permutations (Krebs 1989; Legendre and Legendre 1998).

We further analyzed the estimated similarity of ants at different probe depths, as well as those collected with different methods, to examine how similarity might change if sampling was completed. We used the method of Chao et al. (2005), which has been shown to be less biased than traditional indices when undersampling results in a large number of missing species. Estimated similarity was calculated using the Similarity Index function in the SPADE program (version 3.1; Chao and Shen 2003) for multiple incidence data. Incidence-based adjusted Jaccard values were calculated using 200 bootstrap replications. As in the ANOSIM, species presence/absence data were used to evaluate the similarity of

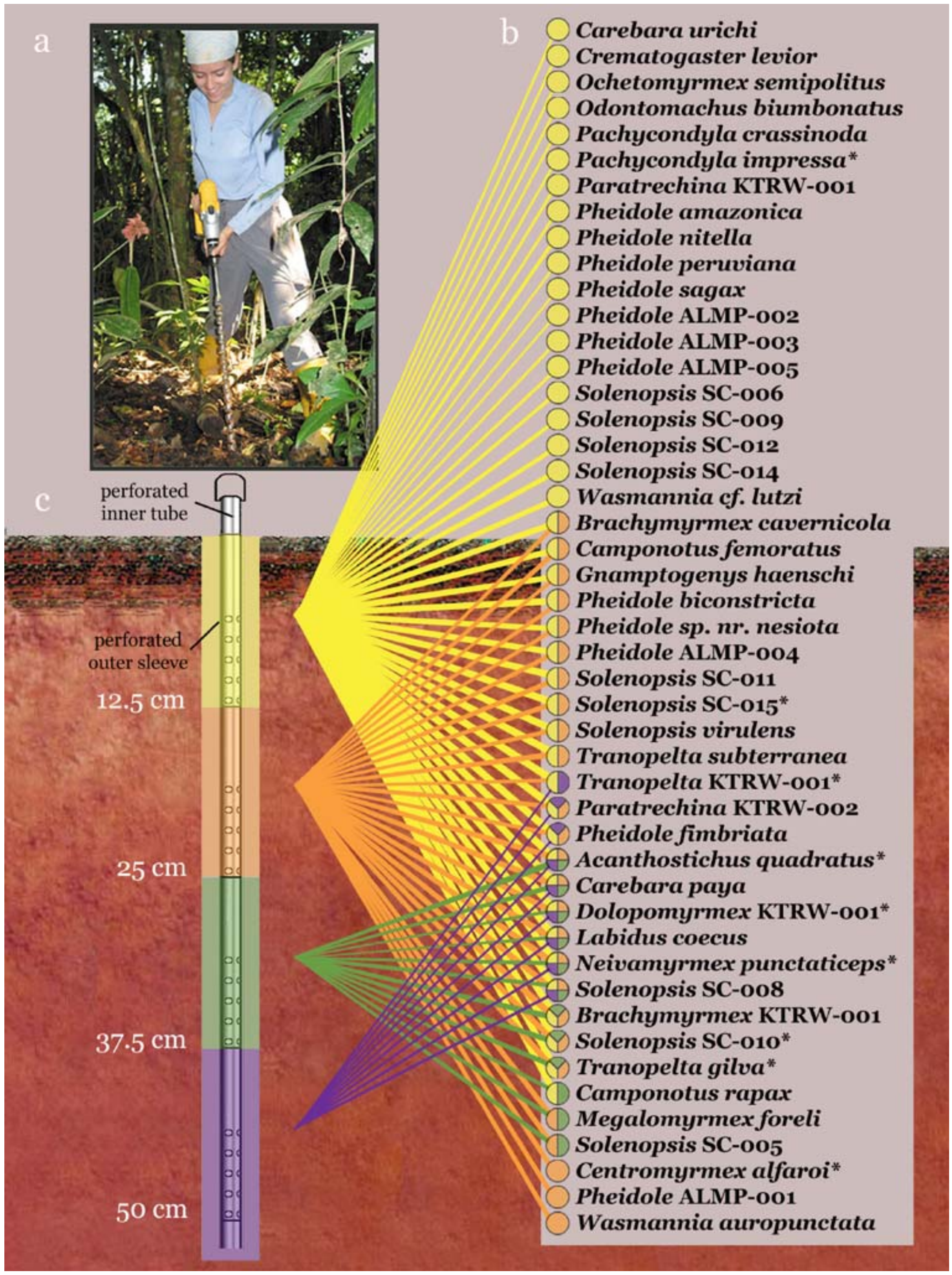

Fig. 1 Sampling the diversity of the soil-dwelling Amazonian ant fauna using a subterranean probe. **a** Preparing to implant the probe with a cordless hammerdrill and auger. **b** Ant species found in probes at different soil depths. Color code for depth distribution: *yellow*, 12.5 cm; *orange*, 25 cm; *green* 37.5 cm; *purple*, 50 cm below the surface. *Asterisks* indicate species unique to probe samples. Provisional morphospecies codes are given for unidentified ants. **c** Schematic of probe showing location of non-traversable bait compartments. Photo credit: Scott Appleby

ants found at different probe levels, while genus presence/absence data were used for the analysis of the similarity of ants collected using different methods.

Results

Forty-seven species in 19 genera were collected from probes (Fig. 1). *Acanthostichus quadratus*, *Centromyrmex alfaroi*, *Dolopomyrmex* KTRW-001, *Neivamyrmex punctaticeps*, *Pachycondyla impressa*, *Solenopsis* SC-010, *Solenopsis* SC-015, *Tranopelta gilva*, and *Tranopelta* KTRW-001 were unique to probes. The megadiverse genus *Pheidole* comprised 25.5% of species collected in probes. Most species (78.7%) were collected within 24 h of placement; after 48 h seven additional species were collected, and three more species were found at 72 h. Maximum richness (42 species) occurred at 12.5 cm below ground, with 26, 12, and 9 species found at 25, 37.5, and 50 cm, respectively. Species richness at the two levels closest to the surface was most similar (44.7%), whereas species collected in the most distant probe compartments (12.5 and 50 cm) were the least similar (21.4%). Six species (12.8%) were found at all four depths, whereas 22 species (46.8%) were found at only one depth (Fig. 1). ANOSIM comparisons showed significant ($p \leq 0.018$) differences between species assemblages 12.5 cm below ground and each of the other three depths. Assemblages collected at other depths were not significantly different. Estimated similarity comparisons revealed the greatest difference in assemblages between 12.5 and 37.5 cm (0.4268), with 12.5 and 50 cm being the most similar (0.7655; Table 1, ant assemblages of different probe levels). However, this result was due to the presence of one species, *Tranopelta* KTRW-001, at the 12.5 and 50 cm depths. When we recalculated estimated similarity treating *Tranopelta* KTRW-001 as an outlier, the greatest difference (0.4363) in assemblages was between 12.5 and 37.5 cm and assemblages found at 12.5 and 25 cm were the most similar (0.7532; Table 1, with *Tranopelta* KTRW-001). Species accumulation rates decreased with depth (Fig. 2). All four curves showed a good fit to logarithmic models ($R^2 \geq 0.8809$).

At least nine species (19.2%) were unique to probes: these ants were not collected using any other method. Other species (*Gnamptogenys haenschi*, *Carebara paya*, *Labidus coecus*, *Solenopsis* SC-012) were relatively common in probes but were only collected in a single nonprobe sample (Table 2). ANOSIM calculations using data on genera revealed all ant assemblages differed significantly by collection method ($p<0.001$). This remained true even when specimens from 12.5 cm below ground were compared with pitfall and/or Winkler collections ($p<0.001$). Estimated similarity calculations of genera showed probe samples and samples obtained from other collection methods were generally more dissimilar than samples collected using other sampling methods were to each other (Table 3). Similarity between probe samples and the other five methods employed ranged from 0.4591 (vs Winklers) to 0.7312 (vs hand collecting), while the similarity between samples using other collection methods ranged from 0.7062 (bait vs Winklers) to 1.0 (bait vs pitfall).

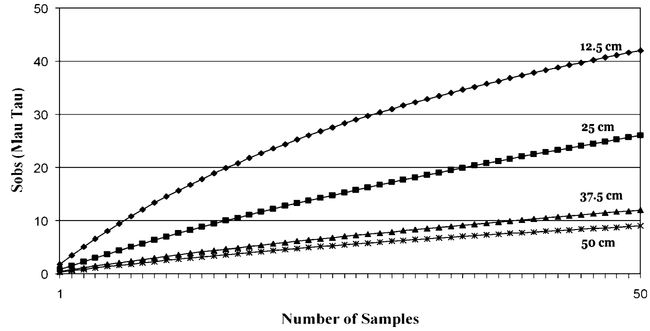

Fig. 2 Accumulation curves of species observed (Sobs Mau Tau) collected at the four probe depths

Discussion

The number of ant species collected, including new and apparently rare forms unlikely to be found using other methods, was substantially increased using subterranean probes. One species, *Dolopomyrmex* KTRW-001, is a new species of a recently described genus found in the Southwestern USA (Deyrup and Cover, in press) that may be wholly hypogaeic (S. Cover, personal communication). *Tranopelta* KTRW-001 has also been identified as a new species (S. Cover, personal communication). *Centromyrmex* and *Acanthostichus*, obligate associates of termite nests and likely predators (Hölldobler and Wilson 1990), are rarely encountered or reported in surveys of tropical ants.

ANOSIM comparisons showed a significant difference between ant assemblages collected using each of the six methods employed. These differences were also found when we compared only the uppermost probe level (12.5 cm) with methods (Winkler and pitfall traps) most likely to collect similar faunas. Comparisons between estimated similarities of assemblages of genera also indicated that subterranean probes captured an assemblage of ants distinctly different from those collected using other methods.

No species were found at the two lower depths that were not also found closer to the surface. One interpretation of this result is that ants found at all four depths may be more generalized in their foraging strategy and/or competitively

Table 1 Estimated similarity between ant assemblages of different probe levels and without *Tranopelta* KTRW-001

	Ant assemblages of different probe levels				Without *Tranopelta* KTRW-001			
	12.5 cm	25 cm	37.5 cm	50 cm	12.5 cm	25 cm	37.5 cm	50 cm
12.5 cm	1.0000				1.0000			
25 cm	0.7377	1.0000			0.7532	1.0000		
37.5 cm	0.4268	0.6470	1.0000		0.4363	0.6470	1.0000	
50 cm	0.7655	0.5149	0.7165	1.0000	0.6250	0.5149	0.7425	1.0000

Table 2 The 47 ant species collected in subterranean probes and their presence in other sampling methods

Subfamily	Species	Found only in probe	Hand collecting	Bait	Pitfall	Winkler	Canopy fogging
Cerapachyinae	*Acanthostichus quadratus*	•					
Ecitoninae	*Labidus coecus*		•[a]				
	Neivamyrmex punctaticeps	•					
Ectatomminae	*Gnamptogenys haenschi*				•[a]		
Formicinae	*Brachymyrmex cavernicola*		•			•	•[a]
	Brachymyrmex KTRW-001		•			•	
	Camponotus femoratus		•	•	•	•	•
	Camponotus rapax		•[a]		•[a]		
	Paratrechina KTRW-001[b]						
	Paratrechina KTRW-002[b]						
Myrmicinae	*Carebara paya*						•[a]
	Carebara urichi		•		•[a]	•[a]	
	Crematogaster levior		•	•	•	•	•
	Dolopomyrmex KTRW-001	•					
	Megalomyrmex foreli		•	•	•	•	•
	Ochetomyrmex semipolitus			•[a]	•	•	
	Pheidole amazonica		•	•[a]		•	
	Pheidole biconstricta		•	•[a]	•	•	•
	Pheidole fimbriata		•[a]			•	
	Pheidole nitella		•	•	•	•	
	Pheidole peruviana		•[a]	•[a]			
	Pheidole sagax		•[a]	•[a]	•[a]	•	
	Pheidole sp .nr. nesiota[b]						
	Pheidole ALMP-001[b]						
	Pheidole ALMP-002[b]						
	Pheidole ALMP-003[b]						
	Pheidole ALMP-004[b]						
	Pheidole ALMP-005[b]						
	Solenopsis SC-005			•[a]		•[a]	•
	Solenopsis SC-006		•	•	•	•	•
	Solenopsis SC-008		•	•	•	•	•[a]
	Solenopsis SC-009			•	•	•	•
	Solenopsis SC-010	•					
	Solenopsis SC-011			•[a]	•	•	•[a]
	Solenopsis SC-012					•[a]	
	Solenopsis SC-014				•[a]	•[a]	
	Solenopsis SC-015	•					
	Solenopsis virulens		•	•	•[a]	•	
	Tranopelta gilva	•					
	Tranopelta KTRW-001	•					
	Tranopelta subterranea		•	•		•	
	Wasmannia auropunctata		•	•	•	•	•
	Wasmannia cf. lutzi		•	•[a]	•	•	•
Ponerinae	*Centromyrmex alfaroi*	•					
	Odontomachus biumbonatus		•[a]		•[a]		
	Pachycondyla crassinoda		•[a]	•	•		
	Pachycondyla impressa	•					

Species found in probes are compared to those collected using traditional sampling methods.

[a] indicates collection in only 1 sample (within each method).

[b] denotes genera for which species identifications (in non-probe samples) are pending. Some *Pheidole* minor workers could not be identified because no corresponding major worker was collected.

dominant, while ants found at only one depth may have a more narrow foraging range or were displaced from baits at other probe levels. Alternatively, ants found at all four levels may be truly hypogaeic, while ants found only in the top layer may nest in the soil stratum but forage mostly on the surface. Although assessing subterranean ant diversity with our probes may be complicated by species interactions, frequent bait inspections could identify "opportunis-

Table 3 Estimated similarity between assemblages of ant genera collected using different techniques

	Bait	Canopy Fogging	Hand Collecting	Pitfall	Subterranean Probe	Winkler
Bait	1					
Canopy Fogging	0.7151	1				
Hand Collecting	0.8733	0.8358	1			
Pitfall	1	0.8922	0.9366	1		
Subterranean Probe	0.5513	0.4749	0.7312	0.689	1	
Winkler	0.7062	0.7591	0.9197	0.945	0.4591	1

Dark cells indicate highest levels of similarity (0.8–1.0); Gray cells indicate similarity scores between 0.6 and 0.8; lowest similar scores (0.4–0.6) are in white cells.

tic" species that arrive quickly but then retreat, or ants having other foraging strategies, and thus provide insight into the structure of the subterranean ant community.

Estimated similarity, in contrast to observed similarity, showed that ant assemblages collected at the largest difference in depth (12.5 vs 50 cm) were more similar if *Tranopelta* KTRW-001 was included in the analysis. *Tranopelta* KTRW-001, however, was the only ant of the total 47 species collected in probes that was found at only 12.5 and 50 cm. We therefore feel more confident in the inference drawn from the observed similarity pattern and the estimate calculated without the inclusion of *Tranopelta* KTRW-001: species assemblages collected at the upper two levels were most similar, and differed most from assemblages collected at the lower two levels (Table 1). In any case, it appears that there is not a unique deep-soil ant fauna at TBS. Although our sample size of 50 probes was modest, species accumulation curves suggested our inventory approached completion 37.5–50 cm below ground, making it unlikely that additional sampling would reveal a distinct community of species below 25 cm. However, studies in different ecological landscapes are necessary to investigate the role that habitat plays in subterranean ant distribution, richness, and abundance. The water table at TBS is relatively high but in a dryer habitat ants may be found deeper in the soil.

Our probes are relatively easy to install with minimal disturbance to the surrounding environment. Because the bait compartments are physically separated, accurate information on the stratification of subterranean species can be acquired. Our technique can also be used to sample other members of the soil invertebrate macrofauna and determine their distribution patterns. Termites, for instance, were commonly found in probe compartments. Our method therefore has wide-ranging applications in biotic inventories as well as behavioral and ecological research on taxa that are among the most diverse and abundant members of the tropical soil fauna. In particular, humivorous termites, which are diverse and abundant in tropical rainforests (Eggleton 2000), could be sampled to gain insight into their cryptic biology. The frequency of censuses, spatial distribution of probes, and bait materials can easily be adjusted to meet research goals.

Vertical stratification appears to characterize ant distribution patterns; the majority of species are associated with only soil, litter or the canopy (Brühl et al. 1998; Vasconcelos and Vilhena 2006; Yanoviak and Kaspari 2000). No one method can ensure the collection of all ants in all strata (Agosti et al. 2000). Therefore, to achieve the most complete survey possible, a combination of methods must be used. Standard methods for collecting leaf-litter and canopy ants are well known (Agosti et al. 2000), but there are few techniques for collecting ants below ground, and no method has emerged as a universal standard. As a result, the subterranean ant fauna has been sampled infrequently and remains largely undescribed. Many subterranean species are known only from a single specimen or series, and their biology is virtually unknown (O'Donnell et al. 2005). Moreover, the Leptanillinae—a clade of entirely subterranean species—is currently considered to be pivotal in ant evolution (Moreau et al. 2006; Brady et al. 2006). Assessing the diversity and sociobiology of this basal subfamily will require sampling methods that specifically target soil-dwelling forms. Implementing the subterranean collecting method we describe can thus enable significant evolutionary and ecological analyses of ants and provide a more comprehensive understanding of the ecology of the invertebrate soil fauna, which in turn may be essential to understanding its role in soil structure and community interactions.

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