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Subterranean Ants

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One of the most conspicuous ecological patterns in ants, especially in tropical regions, is their vertical stratification into distinct arboreal, ground-surface, and subterranean assemblages. The latter are perhaps the least well studied, regarded by some as a frontier in the study of ant diversity [18]. Subterranean ant assemblages harbor a diversity of species with distinct ecologies, including several groups (e.g., Amblyoponinae, Leptaniliane, Martialinae, Proceratiinae) that are evolutionarily distinct from the 90% of species in the formicoid complex [21] and which are important for understanding the early evolution and diversification of ants after the Cretaceous period [10]. Nonetheless, such formicoid taxa as *Acropyga* (Formicinae), *Carebara* (Myrmicinae), and *Solenopsis* (Myrmicinae) are also well represented among subterranean ants with many hypogaeic species (Fig. 1).

Studies on subterranean ants have been restricted to relatively few geographic regions and habitats, a result of longstanding challenges associated with collecting and observing these organisms in the field [23].

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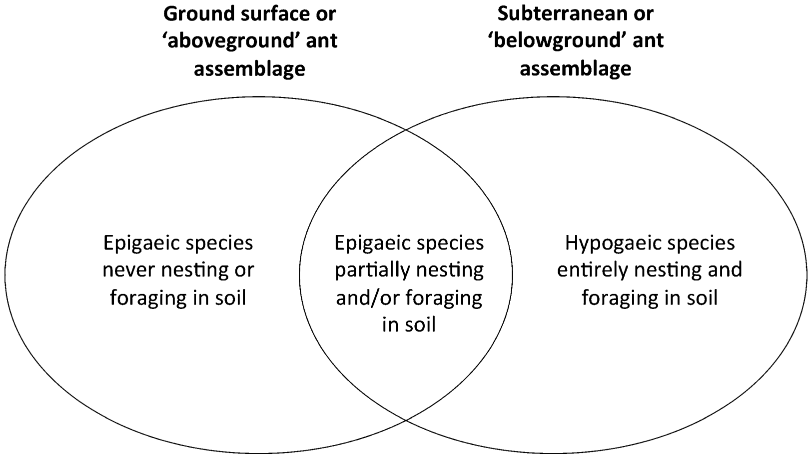
Only Some Ants in the Subterranean Environment Are Hypogaeic

The subterranean, or below-ground, environment comprises the various layers of soil beneath the surface layers of living vegetation and litter. Subterranean ant assemblages comprise a diversity of species reflecting a spectrum of ecological specialization, ranging from epigaeic (surface-dwelling) species that may nest or sometimes forage below ground, to strictly hypogaeic species that nest and forage entirely within the subterranean environment (Fig. 1).

Clear distinctions between ground-surface and subterranean ant assemblages, and between epigaeic and hypogaeic species, may not always be apparent in nature, but they are useful for characterizing the ecological differences among different groups of ants (e.g., [1]). In general, hypogaeic ant species may be distinguished by specialized cryptobiotic morphological traits, which reflect the constraints that the soil's natural pore system places on body size, structure, and mobility. Some common cryptobiotic traits include a depigmented body of relatively small size, reduced or absent spines, short legs, and reduced or absent eyes (Fig. 2). Hypogaeic species are sometimes distinguished by their abundance in samples collected from the subterranean environment relative to those collected from the ground surface [23].

Subterranean Ants, Fig. 1 Schematic representation of the constituents of subterranean ant assemblages with respect to those of ground surface ant assemblages



Subterranean Ants, Fig. 2 *Leptanilla hypodracos*, a hypogaeic species displaying several cryptobiotic traits: a small and depigmented body, and a lack of eyes and spines. Individuals of this species were collected 10–15 cm below ground in Singapore

Estimating the Global Diversity of Hypogaeic Taxa

As most ant species are ecologically poorly known, we used genus-level information in reaching a preliminary, conservative estimate of the global diversity of hypogaeic ant taxa. We first compiled ecological information on all extant genera from the literature and assigned each genus a particular ecological descriptor (e.g., hypogaeic, epigaeic, or arboreal) or a combination of descriptors (e.g., hypogaeic and epigaeic). Next, genera described only as hypogaeic were assumed mainly to contain hypogaeic species; genera with one or more descriptors in addition to hypogaeic were assumed to contain some hypogaeic species; and genera never described as hypogaeic were assumed to contain no hypogaeic species. With this conservative approach, we estimate that 91 ant genera, or 27.2% of the 334 extant genera, mainly contain hypogaeic species and another 48 genera (14.4%) contain some hypogaeic species (Table 1).

However, while 41.6% of ant genera contain hypogaeic species, the species contained within those genera represent less than 27% of all described ant species. This would appear to suggest that hypogaeic ants have diversified poorly in comparison to others and/or that their true diversity is grossly underestimated due to limitations in sampling and taxonomy. It should be noted, however, that in 9 of the 17 extant subfamilies, over 50% of genera contain hypogaeic species (Table 1). Thus, although a hypogaeic lifestyle is widespread across higher taxonomic levels and along the evolutionary history of modern ants [10], it is our working hypothesis that the diversification of ants occurred mainly outside the soil layer and possibly in concert with the diversification of the angiosperms, as suggested by others [12].

Subterranean Ants, Table 1 List of extant ant subfamilies with the respective percentages and numbers (in parenthesis) of genera which mainly contain hypogaeic species, genera which contain some hypogaeic species, and genera which contain no hypogaeic species. Nine subfamilies for which at least 50% of all genera contain hypogaeic species are presented in bold. Two genera were not included as their ecology is unknown

Subfamily name	Mainly hypogaeic	Some hypogaeic	No hypogaeic
Agroecomyrmecinae	50 (1)	0 (0)	50 (1)
Amblyoponinae	55.6 (5)	22.2 (2)	22.2 (2)
Aneuretinae	0 (0)	0 (0)	100 (1)
Apomyrminae	100 (1)	0 (0)	0 (0)
Dolichoderinae	7.1 (2)	3.6 (1)	89.3 (25)
Dorylinae	44.5 (12)	33.3 (9)	22.2 (6)
Ectatomminae	25 (1)	0 (0)	75 (3)
Formicinae	5.9 (3)	2 (1)	92.2 (47)
Heteroponerinae	66.7 (2)	0 (0)	33.3 (1)
Leptanillinae	85.7 (6)	0 (0)	0 (0)
Martialinae	100 (1)	0 (0)	0 (0)
Myrmeciinae	0 (0)	0 (0)	100 (2)
Myrmicinae	25 (36)	16.7 (24)	57.6 (83)
Paraponerinae	0 (0)	0 (0)	100 (1)
Ponerinae	38.3 (18)	23.4 (11)	38.3 (18)
Proceratiinae	100 (3)	0	0 (0)
Pseudomyrmecinae	0 (0)	0 (0)	100 (3)
Total	27.2 (91)	13.8 (46)	58.4 (195)

Diversity of Subterranean Ant Assemblages

The diversity of subterranean ant assemblages at local and regional scales varies substantially across habitats and biogeographic regions. It is also influenced by the volume of past sampling efforts (which remains low in most regions) and the sampling methods used [23]. The most species-rich subterranean assemblages are currently known from the Neotropics, with 113 species from 9 subfamilies in cocoa plantations [6], and 106 species from 4 subfamilies in a fragmented tropical forest [20]. Sampling in multiple habitats across 3 states of the Colombian Amazon region recently recorded 218 species in 10 subfamilies [3], although contamination from other strata occurred due to the methodology used.

While high levels of subterranean ant diversity are often recorded in the tropics, subtropical and temperate regions are also worthy of attention. A recent study in central Florida, USA (28.7°N), found 15 species, including 5 *Solenopsis* species, at high densities in the subterranean environment, with species composition varying with habitat type [15]. Near Beijing (40°N), subterranean pitfall traps operated over several months collect. Near Beijing (40°N), the use of subterranean pitfall traps operated over several months facilitated the collection of two rarely collected genera of Leptanillinae, which significantly expanded their known biogeographic distribution [11]. It should be noted, however, that there is still little targeted sampling of subterranean ant assemblages in most parts of the world, including the Afrotropical, Oceanian, Oriental, and Palearctic realms, and many habitats remain largely undersampled (e.g., grasslands, savannahs, and tropical dry forests) [23]. However, even as they are less diverse than their leaf-litter or arboreal counterparts ([23]; but see [6]), subterranean assemblages possess great ecological and evolutionary distinctness.

Foraging, Diet, and Symbioses

Food resources are likely to be patchily distributed in the subterranean environment. For one thing, subterranean ant colonies, themselves, represent patchy food sources (i.e., as brood) that specialized predators may exploit. Indeed, many hypogaeic ant species are specialized brood predators (e.g., species of *Solenopsis*) and some possess an adaptive army ant syndrome for exploiting this particular resource (e.g., species of *Aenictus*, *Cheliomyrmex*, *Dorylus*, *Labidus*, *Neivamyrmex*). Although many hypogaeic ant species are probably specialized predators [6], some genera (e.g., *Acropyga*) are well known for their symbiotic relationships with honeydew-producing sternorrhynchans (Hemiptera) that feed on plant roots [9]. As food sources, sternorrhynchans are also patchily distributed in the subterranean environment since they cluster around the rhizosphere [6]. While studies on the symbioses between ants and sternorrhynchans below ground have been limited to a few taxa, these associations may be more widespread than previously thought. For instance, Newton and colleagues [13] observed 12 ant species in 4 genera displaying associations with 12 species of aphids and mealybugs in the soils of temperate grasslands, with low levels of specificity to plant hosts.

Above ground, foraging activities of various ant species are often limited by temperature, and many have evolved physiological and behavioral adaptations to cope with heat [4]. However, this situation may be different below ground, because soil not only acts as a buffer against extreme temperatures but also limits daily and seasonal temperature variation [2]. In the New World Dorylinae, the upper critical thermal tolerances (CTmax) of hypogaeic species were 13–15 °C above soil temperatures, yet these values were still significantly lower than the CTmax values of epigaeic species [1, 2]. The buffering effect of soil against varying and extreme temperatures may result in dissimilar foraging and activity patterns between subterranean and surface ant assemblages. For instance, in contrast to foraging patterns of epigaeic dorylines, the foraging rates of hypogaeic dorylines were observed to increase with elevation (and decreasing temperatures) and were also largely unaffected by day-to-day climatic variation [8, 14].

Vertical Gradients Below Ground

Pedological studies have long shown that soils are heterogenous environments where abiotic and biotic properties vary along vertical gradients. For instance, factors such as humidity, temperature, pH, carbon content, and compaction fluctuate along soil depth and influence the abundance, richness, and composition of arthropods along the vertical gradient [17]. As such, the diversity of subterranean ant assemblages can sometimes change significantly over a depth differential of as little as 10 cm soil [15]. In Ecuador, changes in species diversity and composition also occurred along the vertical soil gradient; more diverse assemblages were found near the soil surface than at a depth of 50 cm, with a noticeable turnover in species composition [18]. Similar patterns were observed with subterranean ant assemblages distributed along a vertical soil gradient from 0 to 30 cm in Colombia [3]. Nevertheless, no studies have demonstrably linked the changing diversity of subterranean ant assemblages to specific properties of the abiotic (e.g., pH, temperature) and biotic (e.g., predators, prey) environments with soil depth.

Responses to Environmental Changes and Disturbance

Soil may buffer subterranean ant assemblages from the effects of environmental changes at the surface. For instance, during anthropic fires and infestations by invasive creepers, subterranean ant diversity was found to be less impacted than that of aboveground ant diversity [5, 16]. Subterranean ants are probably affected by disturbances that directly alter soil conditions. One study found that increased soil compaction led to smaller-sized species co-occurring more frequently than larger-sized species [19]. In other studies, however, the extent of soil compaction, as well as other physico-chemical soil properties (e.g., organic matter content, pH, electrical conductivity, degree of humification, soil texture) were poor predictors of the diversity of subterranean ant assemblages [7]. Extensive habitat modification likely impacts subterranean assemblages, as evidenced from changes in their diversity across different land-use types with varying intensification [22]. However, the ecological mechanisms (e.g., specific abiotic and biotic factors) driving these changes remain unclear.

Sampling Subterranean Ants

The use of sampling methods that mainly collect ants from the ground surface, such as pitfall traps and leaf litter extractions, may result in undersampling of subterranean assemblages. Across studies that systematically applied a variety of surface and subterranean methods, the proportion of total ant species unique to subterranean samples varied from 0% to 44% [23]. We recently reviewed specialized field sampling methods for subterranean ant assemblages, which include subterranean baiting, soil sampling, and direct sampling [23]. These various methods are useful for diversity assessments as well as studies on their ecology and behavior.

In conclusion, subterranean ants are among the least studied and most poorly understood groups of ants. Increased targeted sampling of their assemblages across regions and habitats, as well as the development of new methods for collecting and observing the ants in the field, will help to fill current gaps in knowledge of their diversity and responses to abiotic environments. The general life history of hypogaeic species as well as their biotic interactions and functional roles (e.g., as predators and mutualists) in ecological networks below ground are also very poorly known. Future work in these areas may harbor some of the most interesting prospects for ant biology.

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