

ANTS

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INTRODUCTION

Ants are among the most ubiquitous insects on the planet. They occur in all biomes except for the extreme polar regions. In the biomes where ants are abundant, they affect many soil processes that contribute to the creation of patch mosaics that characterize the soils and vegetation of many landscapes. The abundance and diversity of soil-nesting ants varies from as high as 7,000 colonies per hectare in tropical savanna to as few as 3–4 colonies per hectare on some periodically flooded, fine-textured soil, desert landscape units (1). Soil-nesting ants affect critical ecosystem processes such as nutrient cycling and water redistribution. Ant nest mounds vary from a few centimeters in height and diameter to >1 m in height and >2 m diameter (2). Ant nests consist of underground, branched networks of galleries and chambers. Surficial chambers are connected to lower chambers by vertical galleries with branching lateral galleries. Galleries and chambers vary in size and number depending upon the species of ant. For example, *Lasius neoniger*, an abundant ant species in temperate North America, constructs tubular galleries of 1.5–5.0 mm in diameter and chambers of 10–20 mm diameter and 30–50 mm in length. The volume of *L. neoniger* nests range from 20–250 cm³ and are confined to the upper 70 cm of soil (3). Other species construct nests to depths ranging from 50 cm to greater than several meters depending upon species specific behavior, soil type, and landscape position. Soil profile mixing, texture, physical and chemical property modification of mound soils, soil macroporosity, and geomorphological attributes of ant nest mounds vary with species-specific colony longevity, body size, and numbers of workers of a colony, soil type, and landscape position. The perturbation effects of ants are therefore dependent upon the species composition of the ant community, geomorphic history, soil properties, and topographic position of a landscape unit. Because most studies of the effects of ants on soils have focused on one or two species, a comprehensive analysis of the combined effects of all ant species on the soils of an ecosystem cannot be made.

MICROTOPOGRAPHY

In areas that are periodically flooded or where the water table is close to the surface, some species of soil-nesting ants build mounds that create favorable microhabitats for themselves and also a habitat for some species of plants that are confined to the aerated soils of the ant mounds. Soil-nesting ants create hummock microtopography in some wet meadow fens and tropical wet savannas (4). In the Chaco region of South America (parts of Paraguay, Bolivia, Argentina, and Brazil), nest mounds of *Camponotus punctulatus* occur at densities of between 200 and 1000 mounds ha⁻¹. These conical mounds average 0.62 m high (up to 1.85 m high) with a mean basal diameter of 1.2 m. The mound soils are lighter textured than surrounding soils reflecting materials transported from surrounding sub-surface soil during mound construction (5). *Formica podzolica* mounds in a Montana fen are thought to contribute to the hummock-hollow microtopography of peat lands. Abandoned *F. podzolica* mounds provide drier, warmer microsites that are enriched with some soil nutrients (4). The mounds of *Lasius flavus* contribute to the microtopography of some European grasslands and salt marshes (6). Mima-type earth mounds up to 1.5 m in height and 20 m in diameter in the Buenos Aires Province, Argentina, are produced by horizontal translocation of soil to the colony sites of black fire ants, *Solenopsis richteri*. Continued occupation of the mounds by successive generations of ants gradually increases the mounds to mima-type size (7). Ants (*Formica* spp. and *Myrmica* spp.) are important agents in the process of development and maintenance of hummock microtopography of subarctic peatlands. Hummock retrogression is accelerated by the tunneling activity of ants (8).

HETEROGENEITY OF SOIL PHYSICAL AND CHEMICAL PROPERTIES

Many species of ants alter the texture and chemistry of the soil in the nest mounds. The nutrients most frequently

reported to be at higher concentrations in ant mound soils include nitrogen, phosphorus, potassium, calcium, magnesium, manganese, and iron (9). The effect of soil-nesting ants on soil nutrient patchiness and on vegetation varies as a function of landscape position, soil type, and the biology of the ant species. Nutrient enrichment of mound soils has been reported for several species of seed-harvesting ants and omnivorous species of ants that collect seeds, prey on insects, or collect insect carrion. Species of soil-nesting ants that enrich the nutrient content of mound soils are characterized by relatively long-lived colonies (>5 years) and the behavior of depositing chaff and unwanted insect parts on and around the nest mound or disk. Nutrient enrichment of mound soils by a species may not occur on all soils on a watershed or landscape. For example, *Pogonomyrmex rugosus* nest disks in desert shrubland and mixed shrub-grassland were nutrient enriched but the nest disks of this species in a piedmont grassland were not nutrient enriched (10). *Formica* spp. mounds in forest were nutrient enriched but *Formica* spp. mounds in meadows and grasslands were not (11).

The variability in soil nutrient enrichment of ant mounds has been documented in several species of leaf-cutting ants. In remnant Cerrado (woodland-savanna) in Brazil, leaf cutting ants (*Atta* spp.) had no detectable effect on nutrient enrichment (12). In northern Patagonia, soils associated with the leaf-cutting ant, *Acromyrmex lobicornis*, had higher concentrations of nitrogen, phosphorus, and organic matter than reference soils (13). The location of nutrient-rich organic refuse produced by leaf-cutting ant colonies varies among species. *Atta cephalotis* deposit organic refuse in subterranean chambers, whereas *A. colombica* place organic refuse on the soil surface near the nest. The location of organic refuse is a major factor affecting nutrient concentrations and the composition, abundance, and activity of soil microflora and microfauna (14). In the Orinoco Llanos savanna in Venezuela, *Atta laevigata* nests had higher concentrations of nitrogen, magnesium, calcium, and organic carbon, but other soil nutrients and properties were not affected by ant mounds (15).

In an Australia vertisol, ant nest soils had greater concentration of coarse and particulate organic matter, lower fine particulate soil organic matter (SOM)/coarse particulate SOM ratios, larger sand content, and lower clay content than surrounding soils (16). Nutrient enrichment of nest mound soils of funnel ants (*A. barbigula*) was attributed to entrapment of organic materials around the nest entrances. Re-excavation of nest chambers after rainfall buries trapped litter, resulting in higher concentrations of nitrogen, organic matter, and some cations compared to nest-free soils (17). In humid tropical savanna, ant mounds of *Camponotus* spp. had higher clay

and coarse sand content than surrounding soils (9). Even exotic or alien species of ants change the chemical and physical properties of nest mound soils. Imported fire ants (*Solenopsis invicta*) mounds had higher concentrations of clay, phosphorus, and potassium, and lower concentration of soil organic matter, than reference soils. The effect of *S. invicta* on calcium concentrations relative to reference soils was dependent upon the characteristics of the unmodified soil (18).

Ants change the nutrient concentration of mound soils, but the physical and chemical properties of mound soils can also affect mineralization processes. Nitrogen mineralization rates were reduced in nest mound soils in moss-sedge, sedge, and alder peat habitats (19).

SOIL TURNOVER

The longevity and turnover rates of nests and nest mounds of species of ants in a community frequently follow a distribution gradient from high turnover (<3 months) to long-lived (>10 years). The importance of ants in the transport of subsurface horizon materials to the surface varies with the density and diversity of the ant community on a landscape unit. In Chihuahuan Desert grasslands, soil-nesting ants are an order of magnitude more abundant on sand and sandy loam soils than on fine-textured soils. Ants were estimated to move between 21.3 and 85.8 kg ha⁻¹ y⁻¹ on sandy and sandy loam soils and between 0.1–3.4 kg ha⁻¹ y⁻¹ on clay and clay-loam soils (20). The estimated annual soil turnover by ants in an *Atriplex vesicaria* shrubland in the semi-arid region of Australia was 350–420 kg ha⁻¹ y⁻¹ (9). Soil that is excavated by ants in the construction of galleries and chambers and deposited on mounds around nest entrances are generally eroded by water and wind within a year unless the mound is protected from raindrop splash erosion by gravel, stones, or wood fragments. Nest mound soils may be replenished by the belowground expansion of galleries and chambers. Ant nest mounds in sparsely vegetated arid regions are prone to wind erosion. On an Australian aeolian soil, funnel ants (*Aphaenogaster barbigula*) nests were active for approximately 9 months and changed location approximately twice per year. Soil transport was estimated at 33.6 kg ha⁻¹ and it was estimated that 92% of the soil volume would be turned over by these ants in 100 years (21). In western Australia, ant communities on gray soils of semi-arid woodlands were estimated to turnover 46.5 kg ha y⁻¹ and on yellow soils, the soil-nesting ant community was estimated to turnover 22.3 kg ha⁻¹ y⁻¹ (22). In a humid savanna

environment, one abundant ant species, *Paltothyreus tarsatus*, was estimated to transport approximately $30 \text{ g m}^{-2} \text{ y}^{-1}$ of sand particles and soil aggregates. This ant species increased the concentrations of clay, carbon, iron oxides, and coarse sand in the A horizon (9). The amount of soil transported to the surface by *Pogonomyrmex occidentalis* in pinon-juniper woodland and ponderosa pine forest was estimated to be 650 kg ha^{-1} (23). Soil turnover by the ant community in New England forest soil was estimated to be over $50 \text{ kg ha}^{-1} \text{ y}^{-1}$. It was concluded that the translocation of B-horizon materials to the soil surface by soil-nesting ants was an important process in podzol formation in New England forest soils (24).

Some long-lived species of soil-nesting ants relocate their nests one or more times a year. Construction of new nests results in transport to the soil surface of a volume of soil equal to the volume of galleries and chambers. Most of that soil originates in lower soil horizons and contributes to soil profile homogenization. The relocation of nests by some species of ants results in lower estimates of soil turnover than occurs in some environments.

SOIL WATER RELATIONS

The structure of nests of soil-nesting ants provides extensive macroporosity to the soil in which the nests are constructed. The macropores constructed by ants affects rates of infiltration and rates of percolation. In some environments, extremely high densities of nest entrances can have a dramatic effect on infiltration. In semi-arid Western Australia, ant biopores were found to transmit water down the soil profile only when the soil was saturated and water was ponding on the surface (25). On aeolian sand soils in Australian semi-arid woodland, densities of nest entrances of funnel ants (*Aphaenogaster barbigula*) were estimated at $88,000 \text{ ha}^{-1}$. Steady-state water infiltration on soils with nest entrances averaged 23.3 mm min^{-1} , in comparison to an infiltration rate of 5.9 mm min^{-1} on nest-entrance-free soil (26). In semi-arid woodland of eastern Australia on red earth soil, ponded steady-state infiltration averaged 1026 mm h^{-1} on soil with nest entrances of *A. barbigula* but only 120 mm h^{-1} on soils without nest entrances (27). Bulk flow along nest galleries provides an important route of recharge of deep soil moisture in arid and semi-arid environments.

Ant gallery macropores are not always avenues for bulk flow. In a study of a mesic Typic Quartzipsamment, there was no preferential flow down ant galleries. The lack of an effect on hydraulic conductivity was attributed to the sandy soil (28). In another study of a sandy soil, the

estimated saturated soil matrix hydraulic conductivity of nest burrows was approximately eight times smaller than the soil matrix hydraulic conductivity of the bulk sandy soil. This reduction in hydraulic conductivity was attributed to the ants in-filling gallery walls with fine materials (28).

EFFECTS ON OTHER SOIL BIOTA

Soil around relatively long-lived ant colonies may be enriched with microflora, microfauna, and mesofauna. The soils of nest disks of western harvester ants, *Pogonomyrmex occidentalis*, are enriched with vesicular-arbuscular mycorrhizal fungi (29). In areas of North America dominated by the red imported fire ant, *Solenopsis invicta*, the species composition and abundance of soil yeast within mounds are altered by changes in soil properties produced by fire ants (30). Mound soils of *Formica aquilonia* are dominated by bacteria-feeding microfauna and have a higher microbial biomass than surrounding soils (31). Species specific differences in the effect of ants on soil microflora of mounds are related to the feeding strategies of the species and nest architecture. Three ant species, *Myrmica scabrinodis*, *Lasius niger*, and *L. flavus*, differ greatly in foraging strategies and methods of mound construction. Microbial functional diversity and evenness were higher in mound soils of *M. scabrinodis* and *L. niger* than in reference soils but were not different from reference soils in the mounds of *L. flavus*. Different functional groups of microorganisms were activated in the mounds of the different species. Carbon mineralization was higher in mound soils of all three species (32).

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