12.19   Effects of Ants and Termites on Soil and Geomorphological Processes

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Glossary

Calcrete   Hard soil layer composed of calcium carbonate.
Chaff   Dry scaly protective coverings of seeds or similar fine, dry, scaly plant materials.
Epigeic   Aboveground.
Ferricrete   Hard soil layer composed of iron compounds.
Illite clay   Nonexpanding clay composed of silicates.
Microfauna   Primarily protozoans such as amoebae and flagellates.

Microflora   Microbes – bacteria, yeasts, and fungi.
Smectite clay   Family of clays that swell when immersed in water.
Soil aggregate   Group of soil particles adhering together in a cluster.
Suspended sediment   Very fine soil particles that remain in suspension for a long time without contact with the substrate.

Abstract

Ants and termites are one of the most widespread insect groups that occur on all continents except Antarctica. Soil-dwelling ants and termites disturb surface and subsurface soils while constructing their nests and interconnecting tunnels. This soil movement has major effects on soil turnover and development, clay mineralogy, the retention and infiltration of water, and soil chemical properties. The effects of ant and termite activity appear to be greatest for structures that persist for many years. Ants and termites can therefore be regarded as important moderators of soil and geomorphic processes.

12.19.1   Introduction

Ants and termites are social colonial insects whose colonies are typically formed by fertilized queens producing nonreproductive workers. These workers construct the nests, gather food, care for the developing young, and, most importantly, care for the queen. Nests are the central focus of the lives of ant and termite colonies. They house the central food stores and, in some instances, the gardens that provide the energy and nutrient requirements of the colony. Nurseries for the larvae and pupae are an essential component of most nests. Soil-dwelling ant colonies vary in size from as few as 20 to more than 100 000 individual workers. Numbers of

individuals in termite colonies range from 1400 to several million in some of the mound-building species in the tropics (Holldobler and Wilson, 1990).

Workers forage for food in the environment around the nest, a process known as 'central-place foraging' (Bailey and Polis, 1987). This central-place foraging concentrates organic materials in the nest or its immediate surroundings and results in changes in the spatial distribution of organic materials. The distance over which they forage is strongly species dependent and varies with the size of the species and their feeding habits. For example, harvester ants have been known to forage for seeds at distances of up to 20 m from the nest (Gordon, 1992), while other species such as Pheidole spp. in Australia typically forage over shorter distances (Hughes, 1991).

The effects of ants and termites on soil and geomorphological processes result from their tendency to produce resource-rich patterns around the nests, a consequence of their foraging patterns. They are also agents of biopedoturbation (soil disturbance or pedogenesis; Wilkinson et al., 2009), and this disturbance takes many forms. The most direct and widespread form of soil disturbance occurs where they excavate subterranean nests and associated interconnecting tunnels and chambers. The large aboveground structures of many ants and termites are dominant and have long-lived features of some landscapes. The materials used in building these structures have long-term consequences for the development of soil profiles and the creation of soil heterogeneity.

The importance of ants and termites as geomorphic agents depends on their abundance, diversity and species composition, and the density of their nest structures. Most of the studies of bioturbation by ants have focused on species that construct large nests that are occupied by the colonies for more than a decade. Many of these studies have reported effects of these ants on soil chemistry. The bioturbatory effects of ants that build ephemeral nest structures have, however, largely been ignored. The nest cones and mounds of these ants are short lived because they lack structural stability and are easily disintegrated by wind or rain.

In this chapter, we describe the main effects of ants and termites on geomorphology globally, with an emphasis on their effects on soil physical and chemical processes. A substantial amount of our knowledge is drawn from arid and semi-arid landscapes where much of the work on the geomorphic effects of these organisms has been carried out. However, we supplement this with examples from ecosystems worldwide to reinforce the notion that their overwhelming effect is to lead to the formation of nutrient-rich soil profiles.

12.19.2   Geographic Distribution and Diversity

Ants are abundant in most of the world's terrestrial environments from the tropics to the subarctic and from arid to extremely mesic areas (Holldobler and Wilson, 1990). Termites live equatorward of 45–48° N and 45–48° S latitudes. The highest species diversity of ants and termites is in the tropics. For example, in Argentina, the number of termite species ranges from 78 in the wet forests of the Chacoan Province at the Tropic of Capricorn, to 41 to 7 species in the forests, shrublands, and grasslands of the mid-latitudes

respectively. Diversity decreases with increase in latitude to a single species inhabiting the Austrocedrus chilensis forests of the sub-Antarctic region at 45–48° S (Torales et al., 2009). In the Northern Hemisphere, the number of termite species increases exponentially from the Tropic of Cancer (about 20 species) to the Equator (> 60 species) (Goudie, 1988). Diversity even changes markedly over smaller climatic regions. For example, in Israel, the highest ant-species richness occurs at the intersection between two biogeographic regions where resource heterogeneity is likely high (Segev, 2010). In Africa and South America, numerous species occur in tropical rain forest, but in Australia, only four species are restricted to tropical rain forest. In Australia, the termite fauna is more diverse and numerous in dry sclerophyll forests, woodlands, and savannas (Robert, 2007).

In general, ant communities nesting in soils are dominated by small to very small species. For example, the ant fauna on a Chihuahuan Desert watershed are dominated by very small (Forelius spp. and Solenopsis spp.) and small (Dorymyrmex spp. and Pheidole spp.) ants. Ant colony abundance depends on many complex and interacting factors such as topographic position relative to the redistribution of water (e.g., runoff James et al., 2008), soil texture, and vegetation structure and composition. The abundance of soil-dwelling ants may be as high as 7000 colonies ha^{-1} in relatively flat, sandy desert grassland but as few as three colonies ha^{-1} on periodically inundated, fine-textured soils (Whitford et al., 1995). The average density of nests of large seed harvesters that produce ephemeral mounds (Pogonomyrmex californicus and P. desertorum) was 130 ha^{-1} and the average density of the relatively permanent nests of five large species (Trachymyrmex smithii, Aphaenogaster cockerelli, Myrmecocystus spp., Formica perpilosa) was 40 ha^{-1} (Schumacher and Whitford, 1976). The average density of large (5 m tall by 2 m diameter) Macrotermes goliath mounds in tropical rainforests in West Africa is about 17 ha^{-1}. Smaller termite mounds, however, may reach densities of up to 1000 ha^{-1} (Orhue et al., 2007).

12.19.3   Effects of Ants and Termites on Soil Physical Properties

12.19.3.1   Development of Surface and Sub-Surface Structures

Most colonial ants and temperate-zone termites build subterranean nests with either small ($< 1 m^3$) aboveground nest structures or no structures at all. The construction and maintenance of these nests and tunnels of soil-dwelling ants and termites modify soil properties and affect geomorphic processes. Subterranean ant nests generally have a number of descending tunnels that connect to horizontal chambers ranging in shape from oval to hemispherical. The horizontal dimensions of subterranean ant nests commonly exceed more than 2 m (Tschinkel, 2003; **Figure 1**). Similarly, chambers and tunnels of honey-pot ants (Myrmecocystus spp.) have been observed at a depth of 4 m, whereas galleries and tunnels of the subterranean termite Gnathamitermes tubiformans are known to reach depths of up to 9 m (W. Whitford, personal observation). Many tropical and subtropical termite species

Figure 1 Cast showing the nest architecture of the Florida harvester ant (*Pogonomyrmex badius*). Photo by Charles F. Badland.

build aboveground termitaria composed of soil and organic materials. Mounds of tropical termites range in size from a few centimeters in height to as much as 9 m tall and from 6.4 to 9.5 m in diameter (Lal, 1987).

12.19.3.1.1 Elevated ant nests in seasonally flooded environments

The construction of large, tall nest mounds is an important adaptation of ants to seasonally flooded or inundated soils (Figure 2). Nest mounds are produced from soils transported from areas around the mound site. The production of large hummocks and mounds is a characteristic of several species of ants that inhabit wet meadows, fens, peat lands, and tropical wet savannas. For example, the hummock topography of a Montana fen is attributed to the nest mounds of *Formica podzolica* (Lesica and Kannowski, 1998). Subarctic peatland hummock topography is largely formed by the nests of *Formica* spp. and *Myrmica* spp. ants (Lesica and Kannowski, 1998). The hummock topography of some European grasslands and salt marshes are attributed to nest mounds of *Lasius flavus*. These are relatively large ant species that are widely distributed at mid- to high latitudes. In fens, particularly sedge meadows, ant mounds are significant topographic features that provide an important refuge for plant species adapted to drier conditions (Barton et al., 2009). They are also important because they provide habitat for plant species that require well-drained soils.

Figure 2 Large nest of an *Irydomyrmex* sp. ant on a seasonally inundated floodplain in north-eastern Australia. Photo by Melissa Dryden.

In arid areas, the densities of ant nests are known to be greatest in higher elevation positions and lowest at the bottom of the slopes. Lower landscape positions are prone to episodic flooding from upland runoff resulting in fewer species and lower abundances. For example, in the periodically inundated Chaco region of subtropical South America, the dry, vegetated islands are the result of the large (185 cm high, 120 cm across) nest mounds of *Camponotus punctulatus* that occur at densities of between 200–1000 mounds ha^{-1} (Pire et al., 1991). Large mima-type earth mounds (150 cm high, 20 m across) that are prominent topographic features of grasslands of Buenos Aires Province, Argentina, are the result of horizontal transport of soil to the nest sites by black fire ants, *Solenopsis richteri* (Cox et al., 1992).

12.19.3.1.2 Termitaria: Structures of mound-building termites

Mound-building termites are the dominant arthropods of many tropical and subtropical soils. In addition to their nest mounds, many species build foraging galleries or construct sheeting, which is used to cover vegetation and protect the termites against predation while they are harvesting plant material. Most of the nest mounds and galleries are constructed with repacked soil particles collected from the B horizon and mixed with salivary secretions and, commonly, feces. Mounds can be classified according to whether they use orally transported material mixed with secretions or excreta, or whether the material is mainly feces or plant-derived excreta in the construction of their mounds (Orhue et al., 2007) (see Figure 3).

In Botswana, two topographic features (ridges and mounds) have been attributed to the activities of termites (*Odontotermes* spp.). These features occur in cultivated areas and range from 0.2 to 0.8 m above the ground surface (Miller et al., 1994). In tropical semi-deciduous forest, termites build large mounds (1.6 m high, 7–8 m across) around the trunks of dead trees. The volume of these mounds can be up to 50 m^3 (Awadzi et al., 2004). The mounds remain after the tree trunk has disappeared and the termites have left and remain as topographic features for many years.

The most widely studied topographic features produced by termites are the heuweltjies (pronounced *hew-wel-tees*). These mima-like mounds from South Africa are raised areas of finer-textured alkaline soil with enhanced plant nutrients. In the succulent Karoo of South Africa, heuweltjies are thought to have resulted from the foraging and nest-building activities of the termite *Microhodotermes viator*. At a landscape level, heuweltjies resemble a pock-marked pattern that rests above the level of inundation during the wet season (Palmer et al., 1999). They are highly persistent, even after a century of cultivation.

12.19.3.1.3   Stone lines

Layers of stone and coarse material in the soil are known as 'stone lines', three-dimensional (carpet-like) subsurface layers of stones (Johnson, 1989). In Africa, stone line complexes are interpreted by some as being formed entirely or partially by termites, based on the mineralogy similarities of formations above and below the layer, and by the volume of fine particles transported to the surface by termites (Soyer, 1987;

Figure 3   Termitaria from semi-arid woodland in eastern Australia. Photo by D. Eldridge.

Stoops, 1989). Since termites and ants mix and transfer small soil particles to the surface in the construction of nest mounds, stones and prehistoric stone tools and artifacts are commonly displaced downward and ultimately join these stone layers (Johnson et al., 2005). By this mechanism, the biomantle becomes sorted texturally into two layers, an upper layer of fine material over a basal stone layer of coarser material. Although ants and termites are probably important, the origin of stone lines in some areas is probably the result of persistent activities of fossorial vertebrates such as pocket gophers (Johnson, 1989).

12.19.3.2   Soil Turnover and Soil Development

In the process of nest construction and reconstruction, ants pick up soil aggregates, bite off fragments with their mandibles, and relocate the fragments to the walls or tunnels or their subterranean chambers or around the nest entrance. The size of these particles is a function of the size of the mandibles (Sudd, 1969). Thus, the size of particles directly varies with the body size of the ant species (Cammeraat and Risch, 2008).

12.19.3.2.1   Soil turnover by ants and termites

Most estimates of the quantities of soil deposited on the surface by ants come from studies in arid and semi-arid ecosystems. Estimates vary widely, with annual rates ranging from <1 kg ha^{-1} (Whitford et al., 1995) in an arid system to more than 10 000 kg ha^{-1} yr^{-1} in moist tropical ecosystems (Lockaby and Adams, 1985; **Table 1**). Average global rates of soil turnover by ants have been estimated at 5000 kg ha^{-1} yr^{-1} (Folgarait, 1998). The large quantities of soil moved by ants may be of equal or greater importance than earthworms in soil turnover because of their wider geographical distribution, particularly in arid and semi-arid areas. Some ant species move nest entrances frequently (e.g., *Aphaenogaster*; Eldridge and Pickard, 1994; Wilkinson et al., 2009) or build very large mounds (e.g., *Atta* spp.; Bucher and Zuccardi, 1967). Ants

Table 1   Annual rates of subsoil accumulation on the soil surface around the nest entrances of ants

Community	Location	Soil movement (kg soil ha^{-1} yr^{-1})	References
Temperate forest	Massachusetts, USA	60	Lyford (1963)
Rural environments	Berkshire, England	8240	Waloff and Blackith (1962)
Rural environments	New York, USA	948	Levan and Stone (1983)
Rural environments	Wisconsin, USA	11 360	Salem and Hole (1968)
Rural environments	Louisiana, USA	1600[a]	Lockaby and Adams (1985)
Humid savanna	Africa	300	Wood and Sands (1978)
Humid savanna	Africa	4000	Aloni et al. (1983)
Semi-arid woodland	Argentina	1100	Bucher and Zuccardi (1967)
Sown pasture	Argentina	2100	Folgarait (1998)
Sclerophyll woodland	Cataract, Australia	841	Humphreys (1981)
Semi-arid woodland	Cobar, Australia	336	Eldridge and Pickard (1994)
Semi-arid shrubland	Deniliquin, Australia	350–420	Briese (1982)
Arid grassland	New Mexico, USA	0.1–255	Whitford et al. (1995)
Arid shrubland	New Mexico, USA	6.3–35	Whitford unpublished data
Arid dunefield	New Mexico, USA	61.1–187	Whitford unpublished data

[a]One-off measurement only.

with these behavioral characteristics may be responsible for high rates of soil turnover.

In arid environments, the rate of soil deposition also varies with soil texture and bulk density, which affect the energy costs of digging. For example, studies in the Chihuahuan Desert in southern New Mexico have shown that the greatest nest densities and soil deposition rates are on sandy-loam to loamy-sand soils. Similarly, the lowest nest densities and deposition rates by ants were in clay-loam and clay soils that are frequently inundated (Whitford et al., 1995).

Termites also move large quantities of soil from subsoil horizons where constructing sheeting over foraging runways or foraging galleries (Table 2). Rates of gallery sheeting formation from a shrubland in New Mexico ranged from 1000 kg ha^{-1} yr^{-1} on coarse-textured upper slopes to 5650 kg ha^{-1} yr^{-1} on sandy-loam soils in the lower slopes (MacKay and Whitford, 1988). This movement has important implications for the development of soil profiles. Rates of soil deposition in the form of sheeting material range from 2.5 mm per century in seasonally arid tropical grasslands in West Africa to 10 mm per century in tropical woodlands in Northern Australia (Lee and Wood, 1971).

12.19.3.2.2   Effects on soil particle size and clay mineralogy

Material deposited around the entrances of ant nests tends to reflect the texture of the soil layers in which the nests are constructed. In general, there are few general predictions about the textural patterns of the soils deposited in ant mounds. Soils of *Pogonomyrmex rugosus* mounds in southern Nevada sometimes had higher but sometimes lower clay contents than the surrounding soils. Similarly, although mound soils of two seed-harvesting ants (*Messor* spp.) were reported to have higher clay contents than surrounding soils, nests of a functionally similar species *Iridomyrmex greensladei* from Australia had less clay and more sand than the surrounding soils (Nkem et al., 2000). Nest mounds of the European ant (*Lasius niger*) generally have a lower proportion of coarse particles (0.1–2 mm diameter), a lower bulk density (Dostál et al., 2005), and a higher silt content (Cammeraat and Risch, 2008) than surrounding soils. Given that the density of these long-lived ant mounds are up to 5200 nests ha^{-1} (Dostál et al., 2005), their effect on subsoil transport is considerable.

Termite mounds, galleries, and sheeting are constructed with clay, sand, and some silt collected from subsurface soil layers, sometimes cemented using chemical secretions and up to 15% water. Sheeting and mounds therefore comprise predominantly finer-textured materials (e.g., *G. tubiformans*, MacKay et al. (1985); *Macrotermes*, Petts et al. (2009)). Tall-thin *Macrotermes* sp. mounds have clay to sand ratios between 1:1 and 3:1, whereas large-domed *Macrotermes* sp. mounds have clay to sand ratios between 2:1 and 18:1 (Orhue et al., 2007). Termite nests tend to have more clay (generally about 20% more than surrounding soils, e.g., *Odontotermes* in northern Kenya, Bagine (1984); *Amitermes*, *Cornitermes*, *Nasutitermes* in Brazil; Sarcinelli et al., 2009), but sometimes less silt (MacKay et al., 1985). For example, the epigeic nests of mound-building termites, *Cubitermes* sp. mounds, comprised 67% clay and 27% sand compared with adjacent soils, which contained only 31% clay but twice the amount of sand (63%; Orhue et al., 2007).

Construction of aboveground termitaria of *Drepanotermes*, *Amitermes*, and *Nasutitermes* in the Tanami region of north–central Australia results in the transport of fine material into clay-depleted upper soil horizons. These fines are derived from underlying ferricrete and calcrete duricrusts. Soil organic matter and clay particles are primary ingredients of soil aggregates. Thus, anything that affects clay and organic matter will have a major influence on the formation and characteristics of soil aggregates and the movement and retention of ions in upper soil layers. In general, the particle size distribution of termite nest and sheeting material tends to differ from surrounding surface source material. Termites influence the distribution of particle sizes through the differential movement of particular particle sizes, by altering soil aggregation levels and modifying clay mineralogy.

Opinions vary about the origin of the clay present in termite mounds and galleries. Some reports conclude that termites select specific particles from soil horizons below the mound whereas others conclude that soil particles are physically fractured in the guts of the termites. Recent studies (e.g., Jouquet et al., 2002; 2005; 2007) have provided evidence that termites have a direct effect on clay mineralogy. The fungus-growing termite, *Pseudacanthotermes spiniger*, for example, builds subterranean nest mounds to support the fungus-comb structures. These nest structures, foraging galleries, and sheeting are clay enriched. The termites modify these silicate clays through a weathering process, increasing the proportion of

Table 2   Quantities of soil incorporated into the foraging galleries and sheeting over foraging runways by a range of subterranean termites (*Gnathamitermes*, *Odontotermes*, *Dermatotermes*, *Odontotermes*, and *Pseudacanthotermes*)

Community	Location	Soil (kg ha^{-1} yr^{-1})	References
Desert shrubland	Chihuahuan desert, New Mexico	272–498	Whitford et al. (1982) and Whitford (1999)
Desert grassland	Chihuahuan desert, New Mexico	624–2958	MacKay and Whitford (1988)
Humid highlands	Kenya	1059	Bagine (1984)
Semi-arid woodland	Cobar, Australia	656	Whitford et al. (1992)
Savanna	Southern Nigeria	300	Goudie (1988)
Savanna	Senegal	675–900	Goudie (1988)
Tropical grassland	India	5804	Gupta et al. (1981)
Rain forest	Rio Negro, Venezuela	780	Salick et al. (1983)
Savanna	Kenya	1300	Jouquet et al. (2007)

smectite layers and/or reducing the number of clay layers in the crystallites (Jouquet et al., 2005; 2007). This increase in smectites (and corresponding reduction in illite clays) increases the clay's chemically active surface area, resulting in a high cation-exchange capacity. This change in clay ratios affects soil fertility and hydrology (Jouquet et al., 2007).

12.19.3.2.3   Soil profile development or profile homogenization?

The size and aggregate characteristics of the selected soil particles deposited around nest entrances can have significant effects on soil profile development and stability. The effects of ants on the degree of development of soil profiles depend on temperature and rainfall characteristics of nest sites, the type and abundance of ant colonies, and the longevity of their aboveground structures. Many soil-nesting ants modify the soil profile by transporting organic matter to the subsoil or transporting fine particles from deeper layers to the surface during the construction and maintenance of nest galleries, tunnels, and chambers. Their activity, therefore, either can lead to the creation of new horizons from the B horizon material, or can result in the creation of relatively uniform surface horizons in some places (e.g., Wilkinson et al., 2009).

Ongoing transport of finer material to the surface by termites and ants may lead to the creation of distinct organic layers. By removing particles <2 mm in diameter, some tropical mound-building termites such as Cryptotermes sp., Coptotermes intermedius, and Microtermes subhyalinus contribute to development of an ironstone gravel layer below the surface below a gravel-free layer of termite-transported soil (Breuning-Madsen et al., 2007). Whereas the mound and top 15 cm of the soil comprised similar levels of sand, silt, and clay, soils below 15 cm were dominated by 70% gravel (Breuning-Madsen et al., 2007). Similarly, termites in semi-deciduous tropical forest in Ghana construct soil heaps around dead tree trunks (Awadzi et al., 2004). Whereas surface soils in the dead tree mounds contained mainly fine (<1.25 mm) material from the B horizon, material at depth (∼170 cm) comprised predominantly gravel, markedly different from surrounding soil at the same depth (Awadzi et al., 2004). Thus, the termites produced a soil that was markedly different in structure and nutrient content than the surrounding soils. Ants can alter the size range of particles to make them easier to transport to the surface. For example, leaf cutter Attine ants create pellets ranging from 0.5 to 4 mm in diameter, transport them to the surface, and deposit them in a nest-mound pile. These pellets contain plant fragments, silt, and clay particles cemented with clay, producing an organic-rich surface layer (Cosarinsky and Roces, 2007). The rearrangement, sorting, and mixing of soils by termites result in a locally thickened biomantle (Obi and Ogunkunle, 2009). The development of latosols (soils high in iron, silicon oxide, and aluminum oxide) in Brazilian tropical rainforests has been attributed to the long-term action of termites and some secondary movement by ants (Reatto et al., 2009).

The effect of mixing of surface and subsurface materials by ants can lead to homogenization of the soil profile, impeding the formation of soil horizons (Folgarait, 1998; Eldridge and Pickard, 1994). For example, construction of nest entrances by the funnel ant (Aphaenogaster barbigula) in semi-arid eastern

Figure 4   Soil removed by the ant *Aphaenogaster barbigula* covers pine needles that have been moved by overland flow. The nest entrances are about 4 cm in diameter. Photo by D. Eldridge.

Australia (**Figure** 4) leads to a complete mixing of surface horizons to a depth of about 30 cm over a period of about 200 years (Eldridge and Pickard, 1994). In more mesic areas, erosion of the mounds of its conspecific *Aphaenogaster longiceps*, and sediment transport by rainwash and overland flow, leads to the development of a granular topsoil above a finer-textured subsoil (Wilkinson et al., 2009).

12.19.3.3   Soil Porosity, Infiltration and Water Storage

Ants and termites directly influence the hydrological properties of soils by producing macropores; continuous tubes or voids (spaces) in the soil body that are greater than about 0.75 mm in diameter (Bouma, 1992). In soils with numerous macropores, water is transported to the deeper parts of the soil profile more rapidly than predicted by infiltration models based on water movement through the matrix pores (micropores). Matrix pores occur between individual mineral grains and between soil particles, but are not biogenic. The network of tunnels and chambers constructed by ants and termites results in lower soil bulk density (or increased porosity) compared with adjacent soils (Lobry de Bruyn and Conacher, 1990; Dostál et al., 2005).

Most studies of the effects of ants and termites on infiltration have been conducted in arid or semi-arid regions, on single species, and at single locations. The magnitude of the effect of ants and termites on infiltration depends on topographic position, soil texture and structure, the type of ant and termite species, and nest morphology. For example, a landscape-scale study examined differences in infiltration between nests of *Aphaenogaster cockerelli* (a generalist omnivorous ant) and *P. rugosus* (a seed-harvesting ant) in a Chihuahuan Desert watershed (James et al., 2008). Ponded steady-state infiltration rates were 8 times greater on ant-modified soils than on nonnest soils, but the relative effect of ants differed with position in the landscape (James et al., 2008). This study reinforced the notion that the effect of ants on infiltration is site and landscape specific. Topography and species type are also important determinants of ant effects on hydrology. The network of tunnels and chambers that make up the subterranean nests of ants provides a method of bulk flow percolation of water to

deep soil layers. Water moving to deep soil layers is isolated from the water stored in the upper layers, which is commonly lost by evaporation. Soil moisture in soils of harvester-ant (*Pogonomyrmex occidentalis*) nests was consistently greater at depths of 60–100 cm compared with the surface ($<$10 cm) soils over a period of 12 months (Laundre, 2008).

Subterranean termites effect infiltration by producing tunnels at the soil surface that allow foragers to carry plant fragments or organic matter into the nest. Most studies on termites have reported generally increased water infiltration. Mound-building termites in a Columbian forest have also been shown to increase porosity by up to 100% and ant-nest mounds by up to 300%, compared with the area surrounding their mounds (Decaëns et al., 2001). However, the density of functional termite-produced macropores is known to vary both spatially and temporally. Studies of the effects of termites on infiltration have been conducted on plots where termites were eliminated with termiticides (Elkins et al., 1986; Mando et al., 1996; Mando and Miedema, 1997), in areas adjacent to functional termite pavements (Eldridge, 1994), or sites colonized by termites (Tongway et al., 1989). Elkins et al. (1986) demonstrated substantially higher infiltration rates in the Chihuahuan Desert in the presence of termites (88.4 mm h^{-1}) than sites where termites had been removed with termaticides (51.3 mm h^{-1}). Similar results were reported for termite and termite-free sites in the wet–dry tropics of Burkina Faso, West Africa (Mando et al., 1996). In the semi-arid mulga (*Acacia aneura*) woodland in eastern Australia, mounds formed by termites around decaying down logs had infiltration rates almost 10 times higher than the surrounding termite-free soils (Tongway et al., 1989). Finally, Eldridge (1994) showed that surface cementation on the pavements of subterranean termites (*Drepanotermes* sp.) resulted in depressed infiltration rates (6.7 mm h^{-1}), which effectively results in water being shed from the pavements to the annular zone surrounding the pavement (113.2 mm h^{-1}; **Figure 5**). A field experiment and modeling study provided details on variation in abundance of termite-produced macropores and the bulk flow dynamics of those macropores (Leonard et al., 2004). In the Sahelian region of Niger, the area covered by termite sheeting was linearly correlated to the number of foraging holes, which averaged 123 holes m^{-2} of termite sheeting. After a 17 mm rainfall, 70% of the foraging hole macropores had been

Figure 5 The aboveground nest capping of a *Drepanotermes* sp. in semi-arid eastern Australia. The cap is about 1 m in diameter. Photo by James Val.

hydrologically active and 30% had been sealed by some means (Leonard et al., 2004).

12.19.3.4 Soil Erosion

Material from ant nests and termite sheeting consists of fine sand, silt, clay, and small soil aggregates. It is therefore potentially susceptible to removal by wind and water. The relative importance of ant nests to suspended sediments in runoff water likely varies with nest density, volume of nest mounds, and the texture and composition of the mounds (Aalders et al., 1989). Sediment concentrations are generally higher on plots with ant mounds than those without mounds, mainly because ant-removed soil has low levels of aggregation (Cerda and Jurgensen, 2008). For example, erosion rates on plots with ants in an orchard in eastern Spain were 41 kg ha^{-1} yr^{-1} compared with 13 kg ha^{-1} yr^{-1} on plots without ant mounds (Cerda et al., 2009). Similarly, in eastern Australia, Richards (2009) demonstrated relatively high rates of erosion of ant-mounded soil from *A. barbigula* ant-nest entrances.

Sheeting and gallery material of subterranean termites are relatively fragile and susceptible to raindrop impact and therefore splash erosion. The proportion of gallery sheeting dispersed as sediment by splash erosion increases with rainfall erosivity and the quantity of sheeting. Gallery material and surface sheeting connecting the aboreal nests of *Nasutitermes* spp. are relatively fragile and easily eroded during high rainfall. This material contributes significantly to soil erosion and sediment transport in African savannas, with rates of 300–1059 kg ha^{-1} yr^{-1} reported for southern Nigeria, Senegal, and Kenya (Goudie, 1988). Termite sheeting may be substantial in arid areas. For example, sheeting of subterranean termites in eastern Australia has been shown to cover up to 6.6% of the timbered groves and 2.3% of unvegetated inter-groves in semi-arid mulga (*Acacia aneura*) woodlands (Whitford et al., 1992).

Erosion rates of 0.025–0.05 mm yr^{-1} have been reported from aboveground termite mounds in semi-arid woodland in northern Australia, where there were 283 mounds ha^{-1} (Holt et al., 1980). Erosion rates of abandoned termitaria (400 kg ha^{-1} yr^{-1}) were reported to be half that of occupied mounds (800 kg ha^{-1} yr^{-1}) in tropical Upper Volta, Africa (Lal, 1987). The main erosion process was identified as soil creep, with rates of 1163 kg ha^{-1} yr^{-1} from the mound to the corona around the mound (Lal, 1987). Erosional fans commonly surround *Odontotermes* spp. mounds for distances of 10–30 m from the base of the mounds (Goudie, 1988). Eroded mounds are continually repaired by termites as long as the colony is active. When colonies expire, however, the abandoned nest mounds erode rapidly, and the original B horizon material making up the mounds is deposited on the soil surface around the base of the mounds.

Rates of mound erosion are known to be accelerated by foraging by domestic and native animals. Aardvarks (*Orycteropus afer*) dig into termitaria, exposing the interior structures that are less resistant to splash erosion than the clay-rich surface. Elephants destroy termitaria in search of mineral-rich soil, accelerating erosion of the mounds (Goudie, 1988). In Central and southern America, foraging for termites by giant anteaters (*Mymecophagus tridactyla*) and armadillos

(*Dasypus* spp.) destroys the hydrophobic surface crust and accelerates rates of splash erosion (Anacleto, 2007).

12.19.4   Effects of Ants and Termites on Soil Chemical Processes

The chemical composition of mound, gallery, and sheeting soils of soil-nesting ants and termites is largely determined by the chemical composition of the soil horizons from which the material has been derived. Many of the studies on the effects of ants on soil chemistry have been conducted on seed-harvesting ant species in arid, semi-arid environments, and temperate woodlands and grasslands. These studies have focused on large body size, long-lived species that build nest structures which persist for several decades (MacMahon et al., 2000). Seed-harvesting ants are central-place foragers and deposit organic debris and unused seed parts in refuse or chaff piles around the perimeter of the nest or mound. When decomposed, this material is a source of essential elements for plant growth (Folgarait, 1998; Whitford et al., 2008). In tropical and subtropical areas, fungus-culturing Attine ants collect leaves or leaf fragments to use as a growth medium for the fungi that provide food for the colony. These Attine ants build large nest mounds that are maintained by the regular addition of plant and soil materials (Leal and Oliveira, 2000).

12.19.4.1   Effects on Movement of Organic Matter

Ants and termites have their greatest effect on soil chemistry by increasing the organic matter and organic carbon contents of the soils surrounding their mounds (Table 3). Organic matter increase is a result of the use of clay particles by termites in addition to the salivary secretions used by the termites to cement the material together to form their structures (Jouquet et al., 2007). In soils with a higher content of clay,

termites use less organic carbon and nitrogen to construct their sheeting and rely more on clay particles. Organic matter levels in the mounds 3–5 times greater than that in the surrounding soils are not uncommon (Decaëns et al., 2001).

In arid, semi-arid, and some tropical ecosystems, more than half of the potential inputs to the soil organic pool are consumed by termites (Whitford et al., 1992). Organic matter is metabolized more rapidly and effectively by termite gut microflora and microfauna than by free-living microflora and micro- and mesofauna in the soil. Termite feces contain very little humic material. They, therefore, return little of the organic matter that they consume back to the soil. The absence of any natural organic matter pattern in organic matter in arid shrublands and the significant negative correlation between termite abundance and soil organic matter indicate that subterranean termites influence variation in soil organic matter across the watershed (Nash and Whitford, 1995).

Only half of the studies reporting changes in organic carbon concentrations in mound-building termites have reported higher concentrations adjacent to the mounds (Tables 3 and 4). Thus, species such as *Macrotermes bellicosus* that do not use feces in the construction of their mounds produce mounds with lower organic carbon content than the surrounding soil (Abe et al., 2009). This suggests that the origin of higher concentrations of organic carbon in termite-mound soils is via the use of their feces as a cementing agent.

12.19.4.2   Effects on Soil Chemistry

Soils modified by seed-harvester ants generally have higher concentrations of total nitrogen, nitrate and ammonium, total carbon, phosphorus, calcium, and magnesium (e.g., Salem and Hole, 1968; Czerwinski et al., 1969; Mandel and Sorenson, 1982; Petal, 1978, Table 3). Soil pH is, however, generally unaffected by ants (Wiken et al., 1976), though some activity may result in reduced pH in calcareous soils or

Table 3   The numbers of studies reporting effects of different groups[a] of ants on soil chemical properties under or at the edges of the nest compared with adjacent, unmodified soils

Chemical attribute	Seed harvesters			Fungus culturing			Temperate scavengers		
	I	NC	D	I	NC	D	I	NC	D
Soil organic matter	9	2	0	2	0	0	8	1	0
Total N	9	0	0	1	0	1	5	2	6
Nitrate and ammonium	4	0	0	–	–	–	2	0	0
Total C	5	0	0	0	0	4	2	3	0
pH	1	1	4	0	1	1	8	8	1
Total phosphorus	6	1	0	2	2	0	4	0	2
Exchangeable sodium	–	–	–	2	0	1	4	0	2
Exchangeable potassium	2	0	0	5	3	0	6	1	1
Exchangeable calcium	3	0	0	2	2	2	3	3	2
Exchangeable magnesium	3	1	0	1	0	1	4	1	1
Total	42	5	4	15	8	10	46	19	15

I, increased concentration; NC, no change; D, decrease concentration.

[a]Seed harvester ants: *Chelaner* spp., *Messor bouvieri*, *M. Andrei*, *Pogonomyrmex barbatus*, *P. badius*, *P. occidentalis*, *P. rugosus*. Fungus culturing ants: *Atta colombica*, *A. laevigata*, *Trachymyrmex* spp. Temperate zone scavengers: *Camponotus* spp., *C. punctulatus*, *Formica cunicularia*, *F. montana*, *F. rufa*, *F. rufibarbus*, *Lasius flavius*, *L. niger*, *Solenopsis invicta* (an alien fire ant that has invaded the southern United States).

Table 4 Comparison of concentrations of selected soil chemicals in termite-mound soils compared with the concentrations in soils of adjacent pedons

Community	Location	Genus	OC	N	Ca	Mg	K	P	pH
Savanna	Nigeria	*Macrotermes & odontotermes*	I		I	I	I	I	
Savanna	Brazil	Several species	D		I	I	I	I	D
Woodlands	Australia	*Cubitermes & trinervitermes*	I	I				I	
Woodlands	Burkina Faso	*Macrotermes*	D	D					
Woodlands	Australia	*Cubitermes & macrotermes*	I	I	I	I	I	I	I
Desert	Israel	*Anacanthotermes ubachi*		I					
Savanna	Africa	Macrotermitidae			I				I
Savanna	Guyana	Several species			I	I			
Savanna	South Africa	*Microhodotermes*			I			I	I
Savanna	India	*Odontotermes & microcerotermes*			I	I	D	I	
Savanna	Nigeria	*Macrotermes*	D	I	I	I	I		D

OC, organic carbon; N, total nitrogen; Ca, calcium; Mg, magnesium; K, potassium; P, available phosphorus; I, increased concentration; D, decreased concentration.
Source: Data from Orhue et al. (2007), Abe et al. (2009), Zaady et al. (2003).

increases it in acid soils (Folgarait, 1998). Because ants have a marked effect on organic matter around their nests (Table 3), they also influence soluble and exchangeable cations that are adsorbed to the surface of the clay-rich particles (Sarcinelli et al., 2009). The stability of these cations may be influenced by biospheric interactions promoting their release by weathering (Paton et al., 1995; Folgarait, 1998). Soil nutrients also vary with position in the landscape. For example, Sarcinelli et al. (2009) showed that the relative differences in calcium, magnesium, aluminum, and phosphorus between termite-mound and intermound soils increased with distance down the slope.

By far, the greatest effect on soil chemistry results from the activity of harvester ants (Table 3), though the activities of temperate scavenging ants such as *Campanotus*, *Solenopsis*, *Formica*, and *Lasius* generally produce increases in soil cations and soil organic matter concentrations compared with adjacent soils. The effects of fungus-culturing ants such as Atta and *Trachymyrmex*, however, are less clear. Temperate-zone ants from mesic environments provide no consistent patterns of effects on soil chemistry. There are more reports of ants increasing concentrations of soil chemicals than those reporting reductions in concentrations. Some ants may affect soil chemistry by accessing layers of cemented calcrete ($CaCO_3$) to access deeper soil layers (Whitford, 2003; Liu et al., 2007) and bringing this to the surface. For example, the large nest mounds of *Atta vollenweidere* are formed from calcium carbonate-rich soils derived from up to 2 m below the surface (Bucher and Zuccardi, 1967). In the Chihuahuan Desert, fragments of dislodged calcrete are used by seed-harvester ants (*Pogonomyrmex* spp.) and fungus-culturing ants (*Trachymyrmex* spp.) to construct solid caps on the nest mounds. These caps increase the resistance of nest mounds to wind and water erosion, but the calcium may be distributed to other areas through erosion of the nest caps, potentially affecting soil chemistry.

Like the ants, the mound soils of various termite species generally have higher concentrations of organic carbon, total nitrogen and nitrates, available phosphorus and exchangeable calcium, magnesium, and potassium than adjacent soils (Table 4). The effect, however, is generally dependent on soil textural characteristics.

12.19.5 Impacts of Alien Species: The Imported Fire Ant (*Solenopsis invicta*) as an Example

Invasive alien species of social insects have been documented to reduce the diversity of native insects. Some invasive alien species produce impacts that cascade through ecosystems, altering basic ecosystem properties, changing hydrology, nutrient cycles, soil chemistry, and many other biotic and abiotic parameters (Wagner and Van Driesche, 2010). The red imported fire ant, *S. invicta*, is a species that is known to produce dramatic cascading effects on ecosystems in which it has invaded.

S. invicta is a native of South America that was inadvertently released in the southern United States in the late 1930s. *S. invicta* has now spread to 15 states. As *S. invicta* spread across the southern USA, it virtually eliminated the native fire ant, *Solenopsis xyloni*, and markedly reduced the populations of *S. geminata* and the seed harvester, *Pogonomyrmex badius*. In areas with high densities of *S. invicta* colonies, most of the native resident ant species are eliminated (Holldobler and Wilson, 1990). *S. invicta* colonies occur at average densities of 200 ha^{-1} but have been reported to reach densities of 400 colonies ha^{-1} in east Texas (Porter et al., 1991).

Most, but not all, of the ant species reduced or eliminated by *S. invicta* have small, ephemeral, epigeic nests. The main effect of those native resident ant species is soil profile mixing. By contrast, the invasive fire ants construct large mounds that alter the biogeochemical and physical properties of the soils in the areas where they establish colonies (DeFauw et al., 2008). Mound construction by imported fire ant workers results in a dense network of narrow tunnels made of soil pellets transported from deeper soil horizons. The aggregates on the surface of the mounds are less dense and less stable than the adjacent soil aggregates. The fragile crust allows greater infiltration than surrounding soils. Infiltrating water rapidly drains to the deeper tunnels where free water was present between 48 cm–120 cm while the adjacent pedons were dry at those depths (Green et al., 1999). Although imported fire ant nests alter chemical and physical properties of soils, the specific cations and anions concentrated in the nest soils vary with soil type. For example, nest soils in some locations are phosphorus enriched, but in others are not. Calcium and magnesium are concentrated in *S. invicta* mounds in some soils but not in

other locations. In some forest soils, *S. invicta* mounds were higher in organic matter, phosphorus, potassium, and calcium compared to surrounding soils (DeFauw et al., 2008).

Since *S. invicta* reduces the abundance and diversity of native ant species and constructs high densities of large nest mounds, they are a major driver of change in geomorphic processes in areas in which they are dominant. Other ant species that are alien invaders from distant geographic areas have the potential of producing changes in geomorphic processes similar to those that have been documented for the red imported fire ant.

12.19.6 Conclusions

Most of the ecosystems of the planet are subjected to some degree of management by humans, which can have cascading effects on biota and ecosystem processes. There remains, however, a paucity of information on the effects of land management practices on the diversity of ants and termites. Increasing use of intensive agriculture and the use of chemical pesticides are likely to substantially affect populations of ants and termites thereby affecting soil properties, nutrient cycling, and hydrology. Clearing of forest and brush for cultivation results in loss of wood-feeding termites, though fungus-feeding and humus-feeding species are able to survive by foraging in the adjacent agricultural fields (Orhue et al., 2007). Management practices associated with pastoralism appear to have only short-term effects on ants and termites, while fire may have an effect, depending on the community. Fire in some desert grasslands, which is used to increase forage production for livestock or reduce undesirable shrubs, is known to substantially reduce soil deposition by ants and the volume of termite-feeding galleries and sheeting (Killgore et al., 2009). Fire in lichen-spruce woodland in eastern Canada, however, had no appreciable effect on ant colonies (LaFleur et al., 2002). More importantly, projected changes in climate are likely to have a range of effects on ants and termites from changes in their distribution, to altered efficiency of foraging. Increasing temperatures resulting from changing climates may favor the invasion of exotic ant species such as the fire ant (*S. invicta*) at the expense of local ants, with unknown effects on a range of ecosystem services as diverse as soil hydrology and seed dispersal. Despite their small size, a large number of studies have shown that both ants and termites have substantial beneficial effects on ecosystem properties and processes that would be almost impossible to value. Although much has been written about ants and termites, we still know relatively little about their precise roles in soil and ecological processes, their linkages with other biota, and their importance in maintaining healthy and resilient ecosystems (Folgarait, 1998). There is, therefore, an urgent need to quantify some of these unknown effects and to include the study of ants and termites in future studies to develop an integrated understanding of their importance in ecosystem functioning.

Acknowledgments

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