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The effect of ants on soil properties and processes (Hymenoptera: Formicidae)

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Abstract

Ants are ecosystem engineers, greatly affecting physical, chemical, and biological properties of the soil. The effects on physical soil properties are connected with the building of corridors and galleries, which increase soil porosity and may cause separation of soil particles according to their size. Ant-mediated chemical changes of soil are represented mainly by a shift of pH towards neutral and an increase in nutrient content (mostly nitrogen and phosphorus) in ant nest-affected soil. These effects correspond with accumulation of food in the nests and the effect on biological processes, such as acceleration of decomposition rate. Effects on biological soil properties may be connected with increased or decreased microbial activity, which is affected by accumulation of organic matter and internal nest temperature and especially moisture. Effects on the soil vary between ant species; substantial variation can be found in the same species living in different conditions.

Key words: Ants, soil, nutrient cycling, porosity, organic matter, moisture, microbial activity, review.

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Introduction

The role of ants in pest management has been emphasized several times (NIEMELA & LAINE 1986, WAY & KHOO 1992), but much less attention has been paid to the effects of ants on soil properties (CHERIX 1991). In comparison, modification of soil by termites and earthworms is much better understood (LEE 1982, LAVELLE & al. 1997) as is their role in nutrient cycling in ecosystems (JONES 1990). In this review, we will summarize the main mechanisms by which ants affect the soil environment and soil processes.

Ants may build nests, which are used for different periods of time, from several months to decades. Many ants build their nests completely or partly in the soil. The building of such a permanent structure as a nest will affect the properties of the surrounding soil (PETAL 1978, LOBRY DE BRUYN & CONACHER 1990, FOLGARAIT 1998). Ants accumulate a large amount of food in their nests and deposit excreta or food residues inside the nest or in close vicinity, which may alter the nutrient status of the soil. At the same time, food or nest building material is removed from the surrounding ecosystem, and such removal can result in complex interactions. Moreover, ants can directly or indirectly affect other organisms such as aphids, plants, and fungal decomposers, which may lead to complex multitrophic interactions and may also affect soil conditions.

Types of soil nests and bioturbation

Ants build several types of nests in the soil. Soil nests that consist of chambers and corridors can be covered by a stone, dead wood, or some other natural structure on the soil surface. These nests may be surrounded by a crater of the excavated soil, which may also be used to build an aboveground structure, in some species containing both soil and organic material brought from the surroundings. The annual input of plant remains (i.e., coniferous litter) to a *Formica polyctena* nest constitutes 12 - 37 % of the nest volume (POKARZHEVSKIJ 1981). It is generally assumed that ants build aboveground structures for thermoregulation of the nest. Nests built of mineral particles trap solar radiation, which can create large variability in temperatures. In response to this variation, ants can move into that part of the nest that offers the best microclimatic conditions. Ants that build organic anthill nests, especially several species of the subgenus *Formica* s.str., can maintain a relatively constant temperature inside the nest (about 10 °C higher than the ambient temperature) because organic material provides much greater insulation than mineral soil.

Belowground nests typically consist of vertical tunnels that connect horizontal chambers (MIKHEYEV & TSCHINKEL 2004). The descending angle of the tunnels may vary, forming a zig-zag or helix structure (TSCHINKEL 2004, MIKHEYEV & TSCHINKEL 2004). Chambers are built as horizontal appendages or enlargements of tunnels (TSCHINKEL 2004). Chambers may be similar throughout the nest and their size or number may be proportional to the number of workers, as shown by MIKHEYEV & TSCHINKEL (2004) for *Formica pallidefulva*, or more complex rules may apply. *Pogonomyrmex badius* construct top-heavy nests with larger chambers in the shallower parts, most likely due to age division of labor and differences in depth distribution of workers of different age. Older workers are more engaged in digging than younger workers and occur more frequently in the upper parts of a nest (TSCHINKEL 2004).

Tunnels or chambers excavated belowground are coated with fine material in some cases but not in others

Tab. 1: Amount of soil excavated per year and ha by various ant species.

Species	Habitat / Country	Amount of soil	Reference
Formica cf. *picea*	forest / Russia	30 m^3	DMITRIENKO & PETRENKO (1976)
Whole community	prairie / Russia	500 kg	DMITRIENKO & PETRENKO (1976)
Chelaner sp.	prairie / Australia	5 - 6 kg	BRIESE (1982)
Pheidole sp.	prairie / Australia	75 - 90 kg	BRIESE (1982)
Iridomyrmex sp.	prairie / Australia	150 - 180 kg	BRIESE (1982)
Whole community	prairie / Australia	350 - 420 kg	BRIESE (1982)
Pogonomyrmex occidentalis	prairie / USA	2.8 - 8 kg	ROGERS (1972)
Lasius niger	fallow / USA	855 kg	TALBOT (1953)
Whole community	podzol / USA	600 kg	LYFORD (1963)
Myrmica sp.	meadow / Poland	230 - 9,700 kg	PETAL & al. (1977)
Lasius sp.	meadow / Poland	230 - 9,700 kg	PETAL & al. (1977)
Lasius flavus	meadow / Russia	3,000 - 13,000 kg	DLUSSKIJ (1981)

(WANG & al. 1995, COSARINSKY 2006, COSARINSKY & ROCES 2007). Walls of aboveground structures are formed by pellets of excavated material, which are glued together by their edges, leaving star-shaped voids between the pellets (COSARINSKY & ROCES 2007). Sometimes pellets of excavated material may keep their original microstructure, but soil transport may cause separation of materials based on grain size (COSARINSKY 2006). This most likely depends on the preferred load size carried by the ants and the grain size composition of a particular soil.

Two major processes of nest building can be important for soil modification: bioturbation, which involves the mixing and accumulation of soils from different sources and horizons (NKEM & al. 2000), and transport of organic material from the surroundings into the nests as food or building material. Ants can excavate a significant amount of soil from deeper layers and deposit it on the soil surface. For *Formica cinerea*, about 85 % of aboveground nest material came from illuvial soil horizons (BAXTER & HOLE 1967). The overall amount of excavated soil in an area also depends on the number of nests, which may vary substantially. For example, the number of *Formica* s.str. nests in eastern Finland is 2.7 - 2.9 / ha (DOMISCH & al. 2006); for meadows in Denmark, NIELSEN (1986) reported that about 15 % of the area was covered by anthills; finally, nests of *Camponotus punctulatus* in northeastern Argentina may reach a density of 1,800 / ha, and individual nests may be up to 2 m in diameter (GOROSITO & al. 2006), which means that about half of the soil surface is affected by anthills. Macropore production may also be important, depending on the number and size of the nests and on the frequency at which nests are abandoned or the old structures replaced by new ones. In some species, a nest is used for only a few months. For example, MIKHEYEV & TSCHINKEL (2004) expect that nests of *Formica pallidefulva* are replaced each half year. On the other hand, some nests of wood ants, *Formica* s.str., may be used for decades (DLUSSKIJ 1967). Nest lifespan is important particularly when nest density is high because empty space is immediately occupied by new nests (NIELSEN 1986). Bioturbation is likely to be more intensive when ants are forming new nests because the formation of new nests requires the building of many new structures. Even with existing nests, however, bioturbation continues because ants repair eroded chambers, fill abandoned chambers with soil, and dig new ones as a replacement (DLUSSKIJ 1981). Estimates of amount of the soil excavated by ants in various ecosystems are given in Table 1.

Bioturbation can also affect the surrounding vegetation. Continuous heaping of soil may support the persistence of some annual plants that would otherwise suffer from competition in dense meadow vegetation (DOSTAL 2007). The ant environment may also support species with fast root growth or long rhizomes (KOVAROVA & al. 2001, DOSTAL & al. 2005) or even support selection of strains of clonal plants with faster root growth and longer rhizomes (ROTHANZL & al. 2007). In some cases, these bioturbations can substantially change the environment for plant growth. For example, *Formica podzolica* forms hummocks in peatland soils, which have much better aeration than the surrounding peat and serve as a habitat for diverse plant species (LESICA & KANNOWSKI 1998).

Physical properties of soil

Building of tunnels and chambers both above- and belowground increases soil macroporosity (MCCAHON & LOCKWOOD 1990) and reduces bulk density. For example, bulk density in nests of *Pogonomyrmex occidentalis* was 1.47 g / cm^3 compared with 1.54 in the surrounding soil (ROGERS 1972). Reduced bulk density may increase soil aeration and permeability of soil for water (DLUSSKIJ 1967, ELDRIDGE 1993, 1994). The effect on water infiltration, however, can be complex. Nests increase not only soil macroporosity but also organic matter content, which may increase water repellency at low soil moistures. Thus, ant

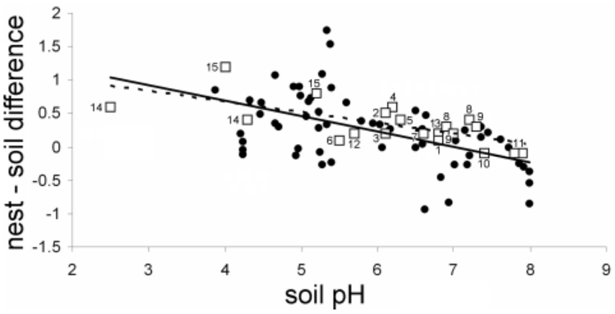

Fig. 1: Relationships between soil pH and the nest-soil difference in pH. Filled circles based on data from *Lasius niger*, according to FROUZ & al. (2003). Empty squares with numbers: 1 - *Formica rufibarbis* according to DLUSSKIJ (1967), 2 - *Formica lugubris* according to MALOZEMOVA & KORUMA (1973), 3 - *Formica polyctena* according to MALOZEMOVA & KORUMA (1973), 4 - *Formica pratensis* according to MALOZEMOVA & KORUMA (1973), 5 - *Formica obscuripes* according to MCCAHON & LOCKWOOD (1990), 6 - *Formica canadensis* according to CULVER & BEATTIE (1983), 7 - *Formica cunicularia* according to CZERWINSKI & al. (1971), 8 - *Lasius niger* according to DLUSSKIJ (1967), 9 - *Lasius flavus* according to DLUSSKIJ (1967), 10 - *Lasius flavus* according to GASPAR (1972), 11 - *Myrmica* sp. according to DLUSSKIJ (1967), 12 - *Myrmica* sp. according to CZERWINSKI & al. (1971), 13 - *Lasius flavus* according CZERWINSKI & al. (1971), 14 - *Lasius niger* according to PETAL (1978), 15 - *Myrmica* sp. according to PETAL & al. (1977). Solid line represents a trend line for *L. niger* (r = 0.517), dotted line represents a trend line for multispecies data (r = 0.668); both significant at $p < 0.01$.

nests increased water infiltration in moist or wet conditions but decreased water infiltration in dry conditions (CAMMERAAT & al. 2002). GREEN & al. (1999) found that macroporosity in nests of imported fire ants can increase drainage, quickly bringing water to deeper soil layers and ensuring higher moisture in soil below the nest while reducing moisture in the nest compared with that in the surrounding soil. *Camponotus punctulatus* nests are surrounded by a peripheral ditch where water accumulates, producing a constantly-wetted zone inside the anthill. Nest moisture is often significantly different from the moisture of surrounding soil and can be lower (MCCAHON & LOCKWOOD 1990) or higher (COENEN-STASS & al. 1980); it varies even within the same species (FROUZ 2000). For example, *Formica polyctena* can have wet and dry nests, which differ in temperature regime and also in the location and intensity of microbial activity, which is related to temperature and moisture content (FROUZ 2000, FROUZ & FINER 2007).

Temperature is another physical factor that is altered in an ant nest, and regulation of internal nest temperature has been mostly described for nests with anthills (DLUSSKIJ 1967, BRIAN 1978, HÖLLDOBLER & WILSON 1990). The most advanced thermoregulation has been described in wood ants, *Formica* s.str. (STEINER 1924, RAIGNIER 1948, DLUSSKIJ 1967, GALLÉ 1973, HORSTMANN 1983, 1990, ROSENGREN & al. 1987, FROUZ 1996, 2000, FROUZ & FINER 2007). Environmental factors influencing nest temperature are primarily air temperature, nest size, and nest moisture (FROUZ & FINER 2007). Maintenance of higher internal nest temperatures is possibly due to a combination of the insulation provided by the nest (GALLÉ 1973, BRANDT 1980, FROUZ 1996, 2000), the trapping of solar radiation by the nest and by ant bodies (FROUZ 2000), and the production of metabolic heat by the ants (HORSTMANN 1987, 1990, HORSTMANN & SCHMID 1986) and by the microorganisms associated with the nest material (COENEN-STASS & al. 1980, FROUZ 2000).

Chemical properties of soil

Many studies have reported significant differences in chemical soil properties between ant nests and the surrounding soil. In general, ants shift nest pH toward a neutral value (Fig. 1), i.e., ants increase pH in acidic soils and decrease it in basic soils (DLUSSKIJ 1967, FROUZ & al. 2003). Some interspecific differences were noted in this context; for example, MALOZEMOVA & KORUMA (1973) found that *Formica polyctena* and *Formica lugubris* shift pH from acidic to neutral values more intensively than *Formica pratensis*. The effect of ants on soil pH and other chemical properties can increase as the nest ages, and the effect is greatest near the nest periphery (ZACHAROV & al. 1981). The mechanism behind the influence of ants on nest pH is not clear, but an increase in pH may result from an increase in basic cations, whereas a decrease in pH may result from an accumulation of organic matter (PETAL 1978, FROUZ & al. 2003).

Changes in N and P content in ant nests have often been reported (FROUZ & KALCIK 1996, LAFLEUR & al. 2002, SNYDER & al. 2002, PETAL & al. 2003, WAGNER & JONES 2004, FROUZ & al. 2003, 2005, KILPELAINEN & al. 2007) (Tab. 2). There are interspecific differences in the accumulation of macronutrients in the nests as seen from measurements of several species in one locality (MALOZEMOVA & KORUMA 1973, BRIESE 1982, JONES & WAGNER 2006) (Tab. 2). On the other hand, nutrient accumulation in a particular species is affected by properties of the surrounding soil and the material used for building the nest. For example, FROUZ & al. (2003) showed that the phosphorus content of *Lasius niger* nests was greater in soils already rich in phosphorus. Beside affecting the total content of nutrients in nests, ants also affect the availability of nutrients; studies of *L. niger* and *Formica* s.str. showed that the increase in total P content in the nest was accompanied by a substantial increase in the available forms of P (FROUZ & al. 2003, 2005). In addition to accumulating easily decomposable substances in the nest (Fig. 2), ants can also increase the availability of P. A shift in nest pH may be also important; as mentioned earlier, ants shift pH towards neutral values, and P availability is highest with near neutral pH (BRADY & WEILL 1999). Increases in total C and organic C (BRIAN 1978) as well as humus in the nest (DMITRIENKO & PETRENKO 1976) have often been reported.
A shift in the content of basic cations (Ca^{2+}, K^{+}, and Mg^{2+}) has often been noted in ant nests, including those of *Lasius* spp. and *Myrmica* spp. (CZERWINSKI & al. 1971, FROUZ & al. 2003, STERNBERG & al. 2007) as well as those of wood ants, *Formica* s.str. (MALOZEMOVA & KORUMA 1973, ZACHAROV & al. 1981). A decrease in N content was detected in nests in soil highly contaminated by nitrogen (PETAL 1978; Tab. 2). This was explained by the increased numbers of soil bacteria that bound N in their biomass. Similarly, there was a lower salt content in nests than in the

Tab. 2: Changes (%) in content of total nitrogen and phosphorus in ant nests compared to the surrounding soil. Content in soil is assumed to be 100 %; – data not available.

Species	N	P	Habitat / Country	Reference
Formica polyctena	167	131	forest / Russia	DMITRIENKO & PETRENKO (1976)
Formica rufa	139	–	forest / Russia	GRIMALSKIJ (1960)
Formica pratensis	–	210	forest / Russia	MALOZEMOVA & KORUMA (1973)
Formica polyctena	–	516	forest / Russia	MALOZEMOVA & KORUMA (1973)
Formica lugubris	–	607	forest / Russia	MALOZEMOVA & KORUMA (1973)
Formica aquilona	278	239	forest / Russia	ZACHAROV & al. (1981)
Formica canadensis	158	139	meadow / USA	CULVER & BEATTIE (1983)
Myrmica sp.	–	129	meadow / Poland	PETAL & al. (1977)
Lasius sp.	–	129	meadow / Poland	PETAL & al. (1977)
Myrmica sp.	65	–	sand pit / Poland	PETAL (1978)
Lasius niger	65	–	sand pit / Poland	PETAL (1978)
Pheidole sp.	153	534	prairie / Australia	BRIESE (1982)
Chelaner sp.	110	1,266	prairie / Australia	BRIESE (1982)
Iridomyrmex sp.	62	100	prairie / Australia	BRIESE (1982)
Solenopsis invicta	100	100	prairie / USA	COX & al. (1992)

surrounding soil in soil with a high content of salt (COX & al. 1992).

For all chemical effects of ant nests, the strongest was observed in the center of the aboveground part of the nest (MALOZEMOVA & KORUMA 1973, ZACHAROV & al. 1981, FROUZ & al. 2003, 2005). In addition, nutrient concentrations and changes in pH increase with nest age (ZACHAROV & al. 1981, WAGNER & al. 2004) and may persist for several years after nest abandonment (JAKUBCZYK & al. 1972, KRISTIANSEN & AMELUNG 2001, KRISTIANSEN & al. 2001, FROUZ & al. 2003).

A question arises – do ants really alter soil chemical conditions or rather do they select soil spots with certain chemical conditions to build their nests? The above-mentioned studies indicated that ants do alter soil properties: nutrient contents follow a consistent pattern inside the nests and increase over time. Moreover, an experiment with an artificial nest (established in the laboratory) showed that ants do change the chemistry of the substrate and deposit specific substances in the nest (CHEN 2005, 2007, LAFLEUR & al. 2005).

Several factors affect the changes in the nutrient content of ant nests in comparison with the surrounding soil. The role of bioturbation is evident if the content of a given element changes significantly with depth of the soil profile. For example, FROUZ & al. (2003) showed that changes in the C content in nests of *Lasius niger* were the most pronounced in forest soil with a shallow but highly organic topsoil. In such conditions, ants substantially reduced the C content in the nest by bringing up mineral soil from deeper layers.

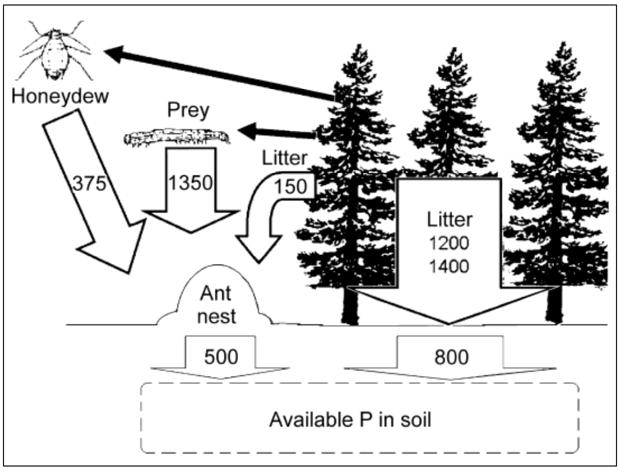

Fig. 2: The effect of the wood ant *Formica polyctena* on P availability (g of P per ha per year) in a forest ecosystem. The upper parts of the scheme represent the flow of total P. The bottom parts summarize the annual input of available P in individual compartments. Based on data from FROUZ & al. (1997).

Ants also collect large amounts of food, and food residues and excreta are important sources of nutrient increase in the nest (PETAL & al. 1977, KLOFT 1978, FROUZ & al. 1997). FROUZ & al. (1997) quantified the flow of P into a nest in the form of food (Fig. 2); their results showed that the amount of P brought annually into the ant nests in 1 ha of forest exceeded the amount of P supplied by annual litter fall. In nests built in organic soil or from organic material, a higher content of available nutrients may be caused by faster mineralisation of organic matter (FROUZ & al. 1997, PETAL 1998, STADLER & al. 2006, WAGNER & JONES 2006). Rapid mineralisation can also explain the higher concentrations of macronutrients in the refuse chamber in *Atta* nests than in the leaf material (GUERRA & al. 2007).

How much of these nutrients that accumulate in the nests can be used by plants? Using ^{15}N, STERNBERG & al. (2007) showed that trees near *Atta* nests used more nest N and contained a higher concentration of Ca than trees more distant from the nests. Similarly, *Acacia constricta* trees near *Formica perpilosa* nests produced more seeds than trees distant from nests (WAGNER 1997). Also, seedlings grew faster and produced more biomass in soil from nests of various ant species, such as *Formica* or *Solenopsis*, than in soil from the surrounding area (FROUZ & al. 2005, LAFLEUR & al. 2005). On the other hand, some field surveys have not shown better establishment of seedlings on ant nests (LAFLEUR & al. 2002). The effect of ants on tree growth may be complex. There are fewer roots below the wood ant (*Formica*) nest than in the surrounding soil but the density of fine roots and macronutrient content of these roots is higher than in the surrounding soil (OHASHI & al. 2007a). This indicates that trees near the nest may use some nutrients stored in the nest. Trees adjacent to a wood ant (*Formica polyctena*) nest grew faster than those 5 - 50 m away but slower than those in a neighboring forest (200 m apart) unaffected by ants (FROUZ & al. 2008). If a substantial portion of the nutrients brought into the nest comes from honeydew (FROUZ & al. 2005, 2008), honeydew depletion may slow the growth of nearby trees (ROSENGREN & SUNDSTRÖM 1991, FROUZ & al. 2008). There are also specific plant species associated with ant nests that usually differ from species growing in adjacent areas (CULVER & BEATTIE 1983). These species must be capable of overcoming the negative effects of the mounds (e.g., the mixing of material) or may benefit from such conditions because of lower competition (DOSTAL 2007).

Biological processes and decomposer communities inside the nest

Ant nests are hot spots of CO2 production and thus are also hot spots of metabolic activity in an ecosystem, as has been repeatedly shown for wood ants *Formica* s.str. (OHASHI & al. 2005, 2007b, RISCH & al. 2005, DOMISCH & al. 2006). CO_2 emitted from the ant nest probably originates mainly from ant respiration, but in some cases microbial respiration may also be important. Microbial activity may be substantially higher in the nest than in the surrounding soil because of a surplus of available nutrients and because of suitable moisture and temperature conditions (FROUZ & al. 1997, FROUZ 2000). Microbial biomass is mostly concentrated in the upper layer of the nest where temperature and moisture are highest (FROUZ & al. 1997, FROUZ 2000). Higher numbers of bacteria, including N_2 fixers, have been found in wood ant nests (GORNY 1976, FROUZ & al. 1997) than in the surrounding soil. In nests of the meadow ants *Lasius* spp. and *Myrmica* spp., counts of bacteria were 14-fold greater and those of fungi 10-fold greater than in the surrounding soil, whereas counts of Actinomycetales were six-fold less than in the surrounding soil (CZERWINSKI & al. 1971). Microbial biomass was also higher in ant nests (DAUBER & al. 2001). In some cases, however, microbial activity in an ant nest may be lower than in the surrounding soil, mainly because of lower moisture in the nest (HOLEC & FROUZ 2006).

Ant nests of *Lasius* and *Pogonomyrmex* have been reported to promote root colonization by arbuscular mycorrhizal fungi (AMF) (FRIESE & ALLEN 1993, DAUBER & al. 2008). This may be due to soil mixing, AMF spore transport, and a more suitable environment (decreased moisture and increased temperature) in the nest (DAUBER & al. 2008).

Other groups of soil biota, including protozoa, were also more abundant in ant nests than in surrounding soil (ZARAGOZA & al. 2007), but the differences are sometimes small (KORGANOVA & RAKHLEEVA 2006). Ant nests may also serve as hot spots for soil invertebrates (LAAKSO & SETALA 1997, 1998).

The effect of ants on soil outside the nest

The effect of ants on the soil surrounding nests is much less understood than their effect on the nest itself, although we can assume that ants can alter soil conditions outside the nest through their foraging activities. The size of the foraging area varies between species and is also affected by colony size, food supply in the habitat, size of workers, and characteristics of the terrain (STRADLING 1978, PETAL 1980). The frequent use of foraging tracks by ants could alter soil properties because ants use such tracks to remove food and because the tracks are often near sites of ant bioturbation (NKEM & al. 2000). Ants may affect soil invertebrates in their territory and, in some cases, may also affect the input of organic matter to the soil. Ants can be important non-specific predators of soil invertebrates, thereby substantially reducing the densities of soil invertebrates, as shown by VINSON (1991) for *Solenopsis invicta* or by HORSTMANN (1970) for *Formica polyctena*. *Formica* ants can collect a significant amount of needles and other plant material and can thus slow litter input to soil. Wood ants also collect a significant amount of honeydew, which may reach up to 719 kg per nest per year (OEKLAND 1930, WELLENSTEIN 1952, HOLT 1955, HORSTMANN 1974, GOEBEL 1988). It seems likely that collection of so much honeydew can alter litter input into the soil. Moreover, ants can also alter litter input to the soil by reducing foliar herbivory (NIEMELA & LAINE 1986).

Conclusion

Because ants affect many soil properties, they are justifiably considered as ecosystem engineers (JONES & al. 1994, JOUQUET & al. 2006). Depending on ant species and soil conditions, ants can either increase or decrease certain soil parameters.

Recent literature provides many examples of differences between ant nests and surrounding soil in physical, chemical, and biological parameters. These examples also show that ants may affect the same parameter in different ways under different conditions. Although the pattern is sometimes clear and consistent (e.g., ants increase pH in acidic soil and decrease pH in alkaline soil), a better understanding of factors that determine how ants influence soil is needed. Most studies have thus far provided descriptive information, and even if the studies presented hypotheses about how the ants alter individual soil properties, they have seldom tested these hypotheses. Thus, future research should test hypotheses so that we increase our understanding of mechanisms underlying how ants affect individual soil properties.

The strongest ant effect has been observed in the ant nest, which represents only a small area in the ecosystem. The effect on the area surrounding the nest is much less understood. This surrounding area is less conspicuous and less defined than the nest, but may include a much larger area. It follows that the impact of ants may be greater in the area surrounding the nest than in the nest itself.

An important research area that has yet to be explored concerns the effect of ants at various spatio-temporal scales of the ecosystem. For example, we know that ants increase available nutrients in their nests. Is the acceleration in nutrient turnover only a local effect? Or do ants deplete the surrounding ecosystem of available nutrients? How do ants affect the spatio-temporal use of nutrients by plants in the surrounding ecosystem? These and similar questions should be addressed by future research. In other words, more research should be focussed on how ants affect processes on the ecosystem level rather than on the level of the individual ant nest.

Finally, ants participate in many multitrophic interactions, such as predation (NIEMELA 1986), protection of aphids (GOEBEL 1988), and seed removal and dispersion (HOWE & SMALLWOOD 1982, ZHOU & al. 2007). How these interactions relate to the effect of ants on soil properties also requires study.

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Zusammenfassung

Ameisen sind Ingenieure des Ökosystems, mit enormem Einfluss auf physikalische, chemische und biologische Eigenschaften des Bodens. Der Einfluss auf die physikalischen Eigenschaften des Bodens steht in Zusammenhang mit dem Bau von Gängen und Gallerien, die die Porosität des Bodens erhöhen und die Auftrennung von Bodenpartikeln nach ihrer Größe bedingen können. Durch Ameisen bedingte Änderungen der Bodenchemie betreffen vor allem eine Verschiebung des pH in den neutralen Bereich und eine Steigerung des Nährstoffgehalts (hauptsächlich Stickstoff und Phosphor). Diese Effekte korrespondieren mit der Anhäufung von Nahrung in den Nestern und der Beeinflussung biologischer Prozesse, beispielsweise der Beschleunigung der Abbaurate. Der Einfluss auf biologische Eigenschaften des Bodens kann mit gesteigerter oder verringerter mikrobieller Aktivität zusammenhängen, welche durch die Anhäufung organischer Substanzen, die Temperatur und insbesondere die Feuchtigkeit im Nestinneren beeinflusst wird. Der Einfluss auf den Boden variiert zwischen den verschiedenen Ameisenarten; eine starke Variation findet sich aber auch innerhalb der Arten, in Abhängigkeit vom Lebensraum.

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