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Wood Ants (*Formica* spp.) as Ecosystem Engineers and Their Impact on the Soil Animal Community

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Abstract

This thesis describes the impact of wood ants on the forest soil biology. The first question addressed is if wood ants affect the ecosystem by concentrating coniferous litter to their mounds. The results suggest that the chemical properties of *Formica* ant nests differ from the surrounding soil, and that the nests are likely to increase the spatial heterogeneity of the forest floor. Wood ants seem to maintain a specific environment in their nests by collecting conifer resin. Resin acts as a carbon source that increases C mineralisation and decreases net N mineralisation. The dry conditions in the ant nests and the addition of resin to the nest material might also determine the composition of soil fauna living in the nests. Collembola seemed to by negatively affected by resin. Oribatids seemed to be unaffected by resin and favoured by low moisture in the nests. The second question was if wood ants affect the soil food web structure by preying upon or interfering with the soil fauna. The results showed that ants can forage on the forest floor during a large part of their active season. This means that ants have a potential to affect the soil fauna in coniferous forests. However, I found little evidence supporting the hypothesis that wood ants have a large impact on the abundance or composition of the soil fauna. In one experiment, the foraging behaviour of wood ants was manipulated by excluding ants from their main protein resources in the tree canopy, with the intention to increase ant activity on the forest floor. When excluded from trees, ants changed their foraging behaviour by searching other trees further away from the nests rather than searching more intensively for prey on the forest floor. In the treated plots (ants excluded from the trees), only Linyphiidae spiders were negatively affected by the ants. This experiment as well as the results of two other studies, indicate that the hypothesis that wood ants are key-stone predators on soil fauna might be rejected. However, to test this hypothesis, more long-term experiments carried out at a large spatial scale are needed.

Key words: Carbon mineralisation, nitrogen mineralisation, conifer resin, foraging behaviour, soil arthropods, soil animal community, Collembola, oribatid mites, Araneae, Coleoptera, natural experiment

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Contents

Statements

There is strong evidence that soil food webs consist of associations of organisms whose trophic relationships are unspecific and variable in time *(Stefan Scheu and Marin Falca. Oecologia (2000) 123: 285-296).*

If, one day, extraterrestrial creatures will visit planet earth, they will not talk with the people. They will try to talk to the real rulers of the world: they will try to talk to the ants *(Bernard Werber. Les fourmis (1991) Editions Albin Michel SA, Paris).*

One fool can ask more questions than ten wise men can answer *(Dutch expression).*

Appendix

Papers I-VII

The present thesis is based on the following paper, which will be referred to by their Roman numerals:

I. Lenoir, L., Persson, T., Bengtsson, J., 2001. Wood ants as potential hot spots for carbon and nitrogen mineralisation. Biology and Fertility of Soils 34:235-240.

II. Lenoir, L., Persson, T., Bengtsson, J., 1999. Effects of coniferous resin on fungal biomass and mineralisation processes in wood ant nest materials. Biology and Fertility of Soils 30: 251-257.

III. Lenoir, L., Persson, T., Bengtsson, J. Effects of conifer resin on soil fauna in potential wood-ant nest materials at different moisture levels. Manuscript.

IV. Lenoir, L., 2002. Can wood ants distinguish between good and bad food patches on the forest floor? European Journal of Soil Biology (in press).

V. Lenoir, L. Effects of red wood ants (*Formica rufa* group) on soil fauna in a coniferous forest. Submitted to Basic and Applied Ecology.

VI. Lenoir, L. Exclusion of wood ants have minor effects on the soil fauna - results from a 4-year experiment. Manuscript.

VII. Lenoir, L. Do ants increase their foraging on the forest floor when excluded from trees? No! Submitted to Ecography.

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Abstract

Lenoir, L., 2001. *Wood Ants (*Formica *spp.) as Ecosystem Engineers and Their Impact on the Soil Animal Community.* Doctor's dissertation.
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This thesis describes the impact of wood ants on the forest soil biology. The first question addressed is if wood ants affect the ecosystem by concentrating coniferous litter to their mounds. The results suggest that the chemical properties of *Formica* ant nests differ from the surrounding soil, and that the nests are likely to increase the spatial heterogeneity of the forest floor. Wood ants seem to maintain a specific environment in their nests by collecting conifer resin. Resin acts as a carbon source that increases C mineralisation and decreases net N mineralisation. The dry conditions in the ant nests and the addition of resin to the nest material might also determine the composition of soil fauna living in the nests. Collembola seemed to by negatively affected by resin. Oribatids seemed to be unaffected by resin and favoured by low moisture in the nests. The second question was if wood ants affect the soil food web structure by preying upon or interfering with the soil fauna. The results showed that ants can forage on the forest floor during a large part of their active season. This means that ants have a potential to affect the soil fauna in coniferous forests. However, I found little evidence supporting the hypothesis that wood ants have a large impact on the abundance or composition of the soil fauna. In one experiment, the foraging behaviour of wood ants was manipulated by excluding ants from their main protein resources in the tree canopy, with the intention to increase ant activity on the forest floor. When excluded from trees, ants changed their foraging behaviour by searching other trees further away from the nests rather than searching more intensively for prey on the forest floor. In the treated plots (ants excluded from the trees), only Linyphiidae spiders were negatively affected by the ants. This experiment as well as the results of two other studies, indicate that the hypothesis that wood ants are key-stone predators on soil fauna might be rejected. However, to test this hypothesis, more long-term experiments carried out at a large spatial scale are needed.

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Introduction

Background

Ants as ecosystem engineers
Although ants may belong to different trophic levels (leaf-cutter and harvester ants are primary consumers, whereas, e.g., *Myrmica* spp. are predators and thus secondary consumers), probably all can be classified as ecosystem engineers (Jones et al., 1994). Ecosystem engineers are organisms that directly or indirectly change the habitat or the availability of resources used by other species (Lawton and Jones, 1995).

Wood ants[1] belonging to the *Formica rufa* group are one of the dominant animal groups in boreal and temperate forests, (Andersen, 1997). They build large nests, and these nests can last for many years (Lobry de Bruyn and Conacher, 1990; Hölldobler and Wilson, 1990). In south Finland, Norway and the southern taiga zone of central Sweden, the colony density of wood ants may be about 4 nests/ha (Rosengren et al., 1979; Swenson et al., 1999) and each nest may have one million workers (Vepsäläinen and Savolainen, 1990; Swenson et al., 1999). Their high abundance as well as the stability of their territories make these insects constant members of the forest ecosystem (Gridina, 1990) and thus an important component (Folgarait, 1998). The impact of wood ants on the forest ecosystem may therefore be considerable (Swenson et al., 1999).

Wood ant nests as habitat for other organisms
Wood ants can regulate the temperature of their nests. The fluctuations in the nest temperature is always smaller than the fluctuations outside the nest (Petal, 1978). For example, in Belgium, the temperature of *F. polyctena* nests ranged from 25 °C to 29 °C, during a period when the average soil temperature was 13 °C (Petal, 1978). The heating of the nest material is a result of insolation (Petal, 1978) and of metabolic activities of the ants (Horstmann, 1990, cit. in Frouz, 1996) and microbes (Coenen-Stass et al., 1980; Frouz, 1996). The moisture conditions in the nests are not as strictly regulated as the temperature (Petal, 1978), but usually wood ant nests are quite dry, compared with the surrounding forest floor (see also paper I).

Because ants transport plant and animal material into their mounds, the nest area often contains high levels of carbon, nitrogen and other nutrients (Hölldobler and Wilson, 1990; Lobry de Bruyn and Conacher, 1990; see also paper I). The continuous input of fresh litter material, resin and prey invertebrates, the high content of waste products and the high temperature inside the nests, make wood ant nests suitable habitats for plants, animals and microorganisms (Lehtinen 1987; Hölldobler and Wilson 1990; Wagner et al. 1997; Laakso and Setälä 1998).

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[1] Wood ants or red wood ants or *F. rufa* group poses a taxonomic problem and some confusion may exists about which ant species belong to the *F. rufa* group (Czechowski, 1993). In this thesis, *F. lugubris* Zett., *F. aquilonia* Yarr., *F. rufa* L. and *F. polyctena* Foerst will be considered as members of *the F. rufa* group

Nests as habitats for plants

In general, plant species composition and relative abundance differ between ant nests and the surrounding areas (King 1977 a,b,c; Horvitz and Schemske, 1986; Lesica and Kannowski, 1998). Anthills may contain fewer common plant species but more rare ones (King, 1977a). Many factors that might positively affect plant growth on ant nests have been mentioned. Ant nests generally have lower bulk density than the surrounding soil (Lesica and Kannowski, 1998), the aeration is better (Lal, 1988) and the temperature on the anthill is high (Lesica and Kannowski, 1998) compared with the surrounding forest floor. Ant hill material may have reduced concentrations of heavy metals like cadmium, lead and nickel (Beattie and Culver, 1983) and have a high nutrient content (McGinley et al., 1994; Wagner, 1997; Lesica and Kannowski, 1998). Many studies have shown that nutrient enrichment can positively influence seedling establishment (Wagner, 1997; McGinley et al., 1994). On the other hand, Horvitz and Schemske (1986) found that although ant nests were significantly enriched in organic matter and nutrients compared to the control soil, seedling growth was not improved by ant-nest soil. Plant growth might be suppressed on nests of some ant species due to low moisture level in the nests (King, 1977a and c). Ants are believed to protect plants against herbivory (Warrington and Whittaker, 1985), but Wagner (1997) and Laakso and Setälä, (2000) found no effect of ants on the levels of folivory and granivory.

Many ant species, among them wood ants, have an impact on the composition of plants growing on their nests by actively dispersing seeds (Baas, 1998). In Europe and North America, 30-40% of the animal-dispersed plants are myrmecochorous. *Viola* spp., *Corydalis* spp., *Silene* spp., and *Anemone* spp. belong to this group (Seifert, 1996). After transporting seeds to their nests, ants eat only the elaiosomes, and the remaining diaspores are disposed in- and outside of the nests (Ohkawara and Higashi, 1994). Ant nests may favour plant species that cannot compete with tall grasses (Dean et al., 1997). Other advantages of myrmecochory for plants are avoidance of seed predation (Ohkawara and Higashi, 1994) or intraspecific competion (Bond and Stock, 1989).

Nests as habitats for soil fauna

Many arthropods live in ant nests as specialised inhabitants of refuse piles, brood or queen chambers, storage areas, or on the bodies of the ants. The relation between ants and myrmecophilous invertebrates ranges from parasitic to symbiotic interactions (Hölldobler and Wilson, 1990; Berg, 1995). Ant mounds covered with plants may allow the development of a rhizosphere-related fauna (Folgarait, 1998). Ant nests are also a suitable habitat for several decomposer animal species (Wagner et al., 1997; Laakso and Setälä, 1998).

In forests, the composition of non-myrmecophilous invertebrates in ant nests differs from that in the surrounding soil (Lehtinen, 1987; Laakso and Setälä, 1998). Laakso and Setälä (1998) found that the microfauna in ant nests of *F. aquilonia* was dominated by bacterial-feeding nematodes, whereas fungal-feeding nematodes were more dominant in the surrounding soil. A large biomass of organisms at the base of the food web (microbes, microbivores and detritivores) was found in ant nests, whereas large predators, other than ants, were fairly scarce. Furthermore, in the forest soil collembolans and mites were equally numerous with many abundant species, whereas several mite species but only two Collembola species were abundant in wood ant nests.

Laakso and Setälä (1998) classified the fauna of ant nests and surrounding soil into clear habitat preference categories. Both habitats harboured many habitat specialists, whereas generalists inhabiting both soil and nests were scarce. The abundance of nest specialists makes the nests important for species richness of the forest ecosystem, especially in poor soils.

Several explanations why the invertebrate ant-nest fauna differs from the soil fauna have been suggested. For example, the anthill material is collected from an area much larger than the area of the nest and during the growing season the input of soil material is continuous (Skinner, 1980; Laakso and Setälä, 1998). The internal environment of the nests might influence the species composition. The surface layer of the nests retains its moisture even during summer droughts (Laakso and Setälä, 1997 and references therein). Gösswald (1981) found that Collembola and Oribatida were numerous in the surface parts of the nests with high organic and moisture levels. The warm and moist nest top layer provided optimal conditions for decomposer microbes, which in turn, can act as a food source for the earthworms that live in the nests. By feeding on fungal mycelia, earthworms may prevent the nest material from becoming interwoven by decomposer fungi and fungal pathogens, thus increasing the longevity of the nest (Laakso and Setälä, 1997). Furthermore, the density and species composition of large invertebrate predators inside the nests differed from that in the soil. This might have contributed to the differences in the composition of fungivores (Laakso and Setälä, 1998).

Nests as a habitat for micro-organisms

A few studies have been carried out on ant-nest-inhabiting micro-organisms and on nutrient and energy fluxes in the nests. There are considerable differences in nutrient content and micro-organism abundances between the nests of different ant species (Jakubczyk et al., 1972; Petal, 1978), resulting in differences in decomposition rate (Petal and Kusinska, 1994). This interspecific variation is probably caused by differences in feeding habits, nest construction and occupation time (Jakubczyk et al., 1972; Petal and Kusinski, 1994). Micro-organisms living inside ant mounds generally utilise detritus i.e. food remnants, faeces, and metabolites (Pokarzhevskii, 1985). Dauber and Wolters (2000) compared microbial activity and functional structure of soil micro-organisms in ant nests of three different ant species, the predator *Myrmica scabrinodis*, the omnivore *Lasius niger*, and the honeydew feeder *L. flavus*. Carbon mineralisation rates were higher inside all ant nests than in control soils, but this was related to stimulation of different components of the microbial community. The authors discussed the relation between active micro-organisms in the nests and food choice of the ants. Nests of *M. scabrinodis* and *L. niger* had more bacteria and fungi, while nests of *L. flavus* had more actinomycetes than the surrounding soil. *L. flavus* promoted micro-organisms that are active during the later stages of decomposition processes (Dauber and Wolters, 2000). Microbial activity in *L. niger* nests decreased in autumn after the shift from high the predatory activity in July to a honeydew based diet later in the year (Jakubczyk et al., 1972; Petal, 1980).

Chemical changes in ant nests

Many studies show an increase in organic matter and nutrient content in ant mounds in comparison to adjacent soil samples (e.g. Umbanhowar, 1992; Frouz et al., 1997; Lesica and Kannowski, 1998; Kristiansen et al., 2000). A likely explanation is that ants collect litter and nutrients from a much larger area than the nests have, thus concentrating resources. Nutrient enrichment has been found more frequently in ant populations that form large, long-lived, stable nests than in populations that relocate their nests frequently (Hughes, 1990), suggesting that ants actively accumulate organic debris over time (Wagner et al., 1997). It has been suggested that the input of carbon and other nutrients as well as the high temperature inside nests might accelerate microbial processes. Decomposition might increase due to N_2 fixation (Frouz et al., 1997). This was shown by a high number of N_2 fixing bacteria and an increase of nitrogenase activity inside the nests of *F. polyctena.* The decomposition of organic matter inside the nests was connected with a high release of phosphorus. Frouz et al. (1997) estimated that 30% of the total P flow from spruce trees into the soil was mediated by ant activity in the nests, which covered only 2% of the forest floor surface. The organic matter content or nutrient concentration vary between nest and the surrounding soil, depending on site location and soil type (Hulugalle, 1995; Whitford and DiMarco, 1995; see also paper I), and the differences seem to be greater in poorer soils (Czerwinsky et al., 1971; Petal, 1992). In infertile environments with low organic matter and complex trophic webs, ants speed up the return to the soil of nutrients held in the bodies of animals (Petal, 1978). Differences in organic matter content or nutrient concentration between nest and the surrounding soil also depend on ant species (Blust et al., 1982; Beattie and Culver, 1983; McGinley et al., 1994; Whitford and DiMarco, 1995).

Some ant species, like wood ants, connect their nests with the surroundings by tracks. Nkem et al. (2000) investigated the impact of nests and trails of *Iridomyrmex greensladei* ants on the surrounding soil environment. The authors stated that 'the frequent use of these tracks by ants could possibly result in alterations in soil properties through excretion, accidental loss of food materials, and even death of individuals' (Nkem et al., 2000). On the other hand, one should not exclude the possibility that ants build their trails along or towards sites with, e.g., high productivity rather than changing soil properties along the trails. López et al. (1993) found that the harvester ant (*Messor barbarus*) constructs trails to sites with high resource availability. Wood ant workers clear trails from vegetation and debris (Hölldobler and Wilson, 1990) and might, thus, alter soil properties on or along trails. As far as I know, no studies have been done on the impact of the extensive trail system of wood ants on soil properties.

Effects of ants on soil fauna

Effects of needle collection on soil fauna

Ants concentrate organic material, e.g., needles, small twigs and conifer resin, on their nest sites. Litter-fall has been estimated to be around 140 to 220 g dry weight m^{-2} in coniferous forests in central and southern Sweden (Persson et al., 1980). A colony of four nests of *F. pratensis* collected 30 kg dry wt of organic material during one season (Pokarzhevskii, 1985). The radius of a territory may be 50 m (Laakso and Selätä, 1998) or even up to 80-100 m (Brüning, 1991; Savolainen, 1991 and ref. therein). This indicates that the needle collection by ants will be only about 1-2% of the litter material present in an ant territory. However, the ants probably do not collect litter and other building materials randomly from the whole territory but from certain spots (L. Lenoir, unpublished observations), possibly leading to local effects of litter depletion.

Litter depletion by ants may affect soil moisture, since litter prevents soil water evaporation. Litter collection can affect the abundance of the litter-dwelling fauna negatively (Tian et al., 1993; Gunadi, 1993 and references therein), which in turn can result in effects on decomposition processes and soil fertility (Gunadi, 1993). Furthermore, soil animals are affected by the chemical features of litter (Tian et al., 1993). Removal of organic matter at a clear-felling stand of a poor pine forest site had long-term negative effects on the abundance of predators, microbi-detrivorous Diptera larvae and fungivorous Collembola. At a more productive spruce site, only predators were affected by removal of organic material (Bengtsson et al., 1998). Ants may collect litter from certain patches and, thus, affect the composition of the soil fauna locally.

Effects of ant predation on soil fauna

The role of ants as consumers is related to their considerable numbers in almost all ecosystems, their socially organised foraging behaviour (Traniello, 1987; Grinida, 1990) and to their high consumption rate (Petal, 1978). Although only 10-20% of the colony members take part in foraging, insect prey is carried into the nest in large quantities. An average-sized colony of *F. polyctena*, which used a territory of 0.27 hectares, captured about 6.1 million animals over the season, which corresponds to 259 MJ of energy (Petal, 1978). The seasonal variation in foraging on invertebrates is high and reflects changes in activity associated with the brood cycle. Maximum foraging probably occurs in the period of the maximum development of new workers. For most *Formica* species there will be a gradual increase in foraging from spring to midsummer, followed by a gradual decrease (Post and Jeanne, 1982; see also paper VI).

Wood ants obtain food from different trophic levels: carbohydrates by collecting honeydew, and proteins by preying upon small animals (Petal, 1978). About 33% (Wellenstein 1952, cit. in Stradling, 1987) to 60% (Pavan, 1979a) of the diet of *Formica rufa* consists of insect prey. The insects collected, e.g. aphids, Diptera, Hymenoptera, Coleoptera, Lepidoptera larvae and Psocoptera, are mainly collected in tree canopies (Rosengren et al., 1979; Cherix and Bourne, 1980; Skinner, 1980; Stradling, 1987). Ants tend to hunt on large, slow-moving arthropods that are easy to capture, and which have a high energy content (Haemig, 1994). The prey items are often recently hatched larvae, larvae immediately after metamorphosis and adults emerging from pupae (Petal, 1978).

Ants hunt on the ground as well as in trees. In *F. polyctena*, 25% of the foraging activity was found to be on the forest floor (Sudd and Lodhi, 1981), and, for instance, Rosengren et al. (1979), Von Sörensen and Schmidt (1987), Brüning (1991) and found that animals as large as earthworms were caught by *F. polyctena*. Kelly and Regniere (1985) found that wood ants were preying upon pupae of the spruce budworm (Tortricidae) on the forest floor. Stradling (1987) stated that wood ants are polyphagous predators, collecting a wide variety of invertebrates and showing versatility in their ability to exploit different resources depending on availability. For example, Godzinska (1989) found that *F. polyctena* and other *Formica* species were hunting Colorado beetles (*Leptinotarsa decemlineata*) in potato fields. It is possible that wood ants prefer to prey on abundant arthropods (Inozemtsev, 1974; Sudd and Lodhi, 1981; Randuska, 1988), which indicates that ants can maintain a high arthropod diversity (Sudd and Lodhi, 1981).

Studies on the effects of ants on soil fauna reveal controversial results. Van der Aart and de Wit (1971) obtained no evidence for ants (*F. rufa*) affecting the spider community. However, some differences in the abundance of a few spider species were found, but they suggested that these changes in numbers might reflect small differences in humidity and in the structure of the vegetation. Brüning (1991) found no significant difference in the density or composition of the spider fauna inside and outside the hunting area of *F. polyctena*. Furthermore, no relation was found between the distance from the ant colony and the number of spiders in the litter layer (Brüning, 1991). On the other hand, Cherix and Bourne (1980), Sudd and Lodhi (1981), Nilsson et al. (1988), Gridina (1990), Niemelä et al. (1992), Punttila, (1994), Oliver and Beattie (1996), Rybalov et al. (1998) and Laakso and Setälä (1998, 1999, 2000) have reported effects of *Formica* spp. on several taxa of soil fauna. A negative correlation has been found between ant abundance and species richness or abundance of beetles (Niemelä et al., 1992; Punttila, 1994; Oliver and Beattie, 1996). Nilsson et al. (1988) suggested that carabid and land-snail diversity on islands was negatively affected by the presence of wood ants. Rybalov et al. (1998) found that wood ants had a negative effect on the abundance of litter invertebrate predators (Carabidae, Lycosidae and Staphylinidae). Sudd and Lodhi (1981) found that ants affected the abundance of Araneae, Coleoptera, Arthropleona, Myriapoda and larval Diptera negatively. Hymenoptera, Acarina and Symphypleona were positively affected. Ants did not affect total numbers of Opiliones, Diptera, Chelonethi and larval Coleoptera. Some spider and harvestmen species increased their numbers in the presence of wood ants, and some showed a reduction. Differences in the effects of wood ants were found not only between species but also between the responses of the same species in different years (Sudd and Lodhi, 1981). Grinida (1990) found that the number of harvestmen in a spruce-pine forest was positively affected by *F. polyctena*, while in a mixed broadleaf/coniferous forest no effect of wood ants on harvestmen was found. In both types forest, the number of Linyphiidae spiders was negatively affected by wood ants, but this effect was much greater in the spruce-pine forest. Laakso (1999) and Laakso and Setälä (2000) found that the effects of ants on the soil fauna were relatively weak and that the direct impact of wood ants on the soil fauna food web was likely to be small. Experimental elimination of wood ant nests (Laakso and Setälä, 2000), resulted in a 90% reduction of ant density. This reduction resulted in an increase of, on average, 67% and 60% of the biomass of predators belonging to the meso- and macrofauna. The biomass of the lumbricid *Dendrobaena octaedra* was 54% higher in plots with high ant density. No differences in species or trophic group composition were found between plots with high and low ant density.

Effects of wood ants as competitors with other ant species

Wood ants compete with other ant species for food and suitable nest sites. Lesica and Kannowski (1998) found that *Formica* and *Myrmica* ant species probably compete for suitable nest sites, resulting in a lower density, but not nest volume, for the smaller and presumably subordinate species. For the foundation of new nests, wood ants often colonise nests of *F. fusca* (Punttila et al., 1991, 1996). Wood ants might exclude each other and suppress the number of other aggressive species, whereas submissive species are less affected (Vepsäläinen and Savolainen, 1990; Punttila, 1994; Punttila et al., 1996). The submissive ant *F. fusca* suffered from reduced food intake close to nests of *F. polyctena,* which can rob large food items from *F. fusca* (Savolainen, 1991). In the presence of *F. polyctena*, *F. fusca* prey upon much smaller insects than in the absence of wood ants. *Myrmica* spp. are able to coexist with, e.g., *F. polyctena* by shifting their foraging activity to night time and by shifting from surface ground to litter and shrub layers (Savolainen and Vepsäläinen, 1989; Vepsäläinen and Savolainen, 1990). When the foraging areas of certain species of ants overlap, spatial avoidance by foragers is observed and subordination to the dominants consists of releasing prey objects without a struggle (Pisarki, 1973 cit. in Petal, 1978). *F. aquilonia* affected the ant community as a whole by competitive suppression, especially in old forests. *F. aquilonia* and *F. lugubris* excluded each other in an old-growth (>140 years) forest and the number of subordinate ant species (e.g. *Myrmica* spp., *Leptothorax* spp. and *F. fusca*) was significantly larger when territorial species were absent (Punttila et al., 1991).

Effects of wood ants on above-ground fauna

Ants can affect the composition of arthropods in the tree canopy and on tree trunks, where they prey upon, interfere or compete with other invertebrates and tend some species of aphids (e.g. Douglas and Sudd, 1980; Skinner, 1980; Skinner and Whittaker, 1981; Haemig, 1994; Halaj et al., 1997). Warrington and Whittaker (1985) showed that wood ants not only affect the number of herbivorous insect species in the canopy, but also the composition of the Lepidoptera community. Haemig (1994) demonstrated that wood ants (*F. aquilonia*) reduced the biomass of arthropod prey in the trees, thus competing with insectivorous birds.

Ants on one hand, and some aphids species on the other, have reciprocal mutualistic relations. Spiders, as general predators, forage on aphids and ants protect their source of carbohydrates by killing or chasing spiders (Heikkinen, 1999). Direct effects of predation on spiders by ants might be negligible (Cherix and Bourne, 1980; Halaj et al., 1997), but the abundance of spiders in the canopy might be negatively affected by interference competion with wood ants (Halaj et al., 1997). This observation is in contrast to that of Karhu (1998) who found no effect of *F. aquilonia* on spiders living in the canopy of white birch (*Betula pubescens*). On the other hand, Karhu found a negative effect of wood ants on the abundance of syrphid larvae, predatory on aphids.

Ants can move cultures of aphids to younger parts of the plants with better sap composition (de Bruyn and Mabilis, 1992). Aphids prefer young plant tissues that are rich in elements as nitrogen, phosphorus, potassium, copper and zinc (van Emden, 1969, cit. in Petal, 1978). The increase in the number of aphids and in the amount of sap consumed by them, which is stimulated by ants, probably increases the rate of cycling of plant nutrients (Petal, 1978).

Ants can also benefit the aphid host plants by removing herbivorous insects (Messina, 1981; Skinner and Whittaker, 1981; Warrington and Whittaker, 1985). Warrington and Whittaker (1985) showed that ants reduced leaf damage on sycamore (*Acer pseudoplantanus*) shoots by predating on Lepidoptera larvae. However, ants can also indirectly harm the plants by protecting homopterans (Klimetzek and Wellenstein, 1978; Ryti, 1992). Klimetzek and Wellenstein (1978) showed that pine trees near nests of *F. polyctena* had reduced height and radial increment. This was suggested to be due to the presence of tended aphids in pine trees near the nests.

Wood ants, in particular *F. aquilonia, F. polyctena* and *F. rufa*, are so effective as predators on pest insects, like sawfly larvae, that they have been used in Europe for centuries to control forest pests (Finnegan, 1975; Pavan, 1979b; Skinner, 1980; Skinner and Whittaker, 1981; Hölldobler and Wilson, 1990). A colony of *F. rufa* gathered 217 000 sawfly larvae and moth caterpillars in a single day (Strokov, 1956 cit. in Hölldobler and Wilson, 1990). Similarly, *F. polyctena* was so effective in protecting mountain birch (*Betula pubescens tortuosa*) against an outbreak of the geometrid moth *Oporinia autumnata* that green islands of intact trees, 40 m in diameter, were left around each nest in the midst of a grey, mostly defoliated forest (Laine and Niemelä, 1980 cit. in Hölldobler and Wilson, 1990). The foraging range of an individual wood ant may exceed 100 m, but a significant effect on defoliating insects ranges occurred only up to 50 m from the nest (Wellingstein cit. in: Rosengren et al., 1979). Species with large numbers of individuals, e.g., *F. polyctena* were even more effective than monogynous species like *F. rufa* (Wellenstein, 1973; Niemeyer, 1976). Karhu (1998) found that outbreak populations of *Oporinia autumnata* were reduced. Rosengren et al. (1979) stated that wood ants are probably important in forest protection by preventing heavy outbreaks of noxious insects and, thus, act as a stabilising factor in the forest ecosystem.

Objectives

The general objectives of this thesis were to determine (1) if wood ants affect ecosystem processes by concentrating coniferous litter to their mounds, and (2) if, wood ants affect the soil food web structure by preying upon or interfering with the soil fauna.

The specific objectives were:

1. To compare the chemical properties and C and N mineralisation rates in the forest floor and in ant nest materials of red wood ants (paper I).
2. To determine the effect of conifer resin and the moisture conditions on C and N mineralisation (paper II) and the decomposer soil fauna (paper III).
3. To investigate if wood ants can forage on the forest floor (paper IV).
4. To determine to which extent wood ants affect the abundance of soil fauna and the composition of soil fauna species in the ant territory (paper V, VI and VII).

The experiments

Chemical properties of ant nests (paper I)

Materials and Methods

To compare the chemical properties of wood ant nest with the surrounding forest floor, soil litter and anthill materials were collected from two different sites, Jädraås in central Sweden and Sunnersta, near Uppsala, in central Sweden. The forest at Jädraås is dominated by Scots pine (*Pinus sylvestris* L.). whereas the forest at Sunnersta is a mixed forest, dominated by Scots pine, Norway spruce (*Picea abies* (L.) Karst.) and birch (*Betula pendula* Roth). The soils had a relatively low pH at Jädraås and a high pH at Sunnersta. At each site, six anthills were selected. Anthill materials were sampled from the top and the centre of the nests at about 40-cm depth below the top. Forest floor materials of 5-6 different cores were sampled about 10 m from each nest. The sapmles consisted of litter and fragmentation material of the ectorganic layer. All materials were homogenised by sieving through a 6-mm mesh.

Results

Nests were always drier, had a higher C/N ratio and often higher ammonium concentrations. At Jädraås, the centre material always had higher ammonium and nitrate concentrations than the corresponding top and soil materials. Inorganic N varied considerately, both in the anthill material and in the soil. At Sunnersta, the top material had, on average, a higher ammonium concentration than the other materials, but the variation was so great that these differences were not significant. At Jädraås, soil pH was lower and at Sunnersta, soil pH was higher than in the nests. These results showed that the chemical properties of wood ant nests differ from the surrounding soil and the nests are likely to increase spatial heterogeneity of the forest floor. The results suggest that the differences in soil properties determine the directions in which ant nests differ from the surrounding soil.

The effect of moisture level on C and N mineralisation in ant nest material (paper I)

Material and Methods

To compare potential C and N mineralisation in ant nest material with mineralisation in forest soil, an incubation study was carried out (paper I). The fresh materials were placed in plastic containers with a 50-cm^2 surface area. Ants were removed, but other soil fauna and microorganisms were kept in the containers. To investigate the effect of low versus high moisture levels, the materials were incubated at two moisture levels, 60% of the water-holding capacity, WHC, in one series and 15% WHC in another series. Moisture can be as high as 60% in the forest floor during early spring and late autumn, while the moisture in anthills is much lower during the whole year. CO_2 evolution was initially measured weekly and after one month every second week. Destructive samples were taken after 50 and 105 days to estimate, e.g., ammonium and nitrate concentrations.

Results

As expected, the C mineralisation rate was higher in the high than in the low moisture treatment at both sites (fig. 1). Increased moisture levels in the anthill material resulted in a net N immobilisation, while surrounding litter material showed net N mineralisation during the study period (fig. 2). It was suggested that dry conditions in the nest material prevented it from being decomposed and, since there were no plants to take up nitrogen, inorganic N accumulated. The results suggest that ant nests do not produce large amounts of inorganic N as long as the ants bring fresh litter with high C/N ratios to the nests and keep the nests dry. However, the nests can be considered as potential "composts" which probably decompose faster and are a source of N leaching when the ants no longer maintain the specific dry conditions.

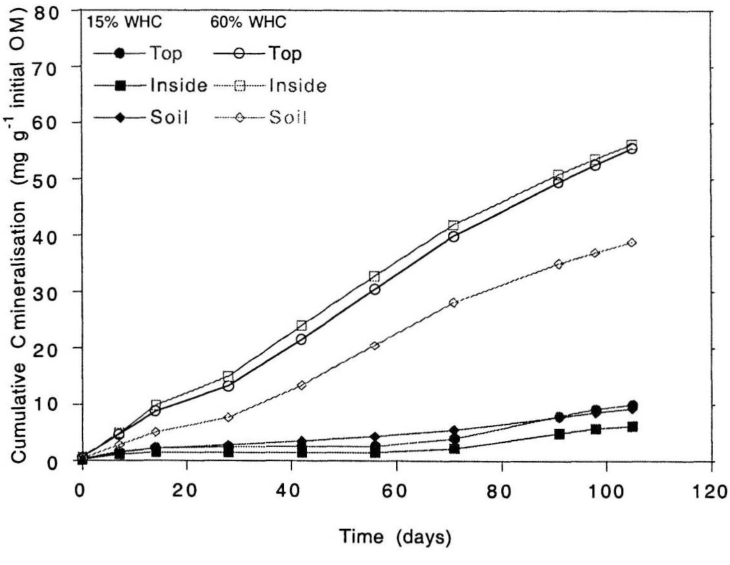


Figure 1. Cumulative C mineralisation in materials from the top and the centre (inside) of wood ant nests and the forest floor (soil) outside the nests at Jädraås at low (15% water holding capacity: WHC and high (60%) moisture. OM organic matter.

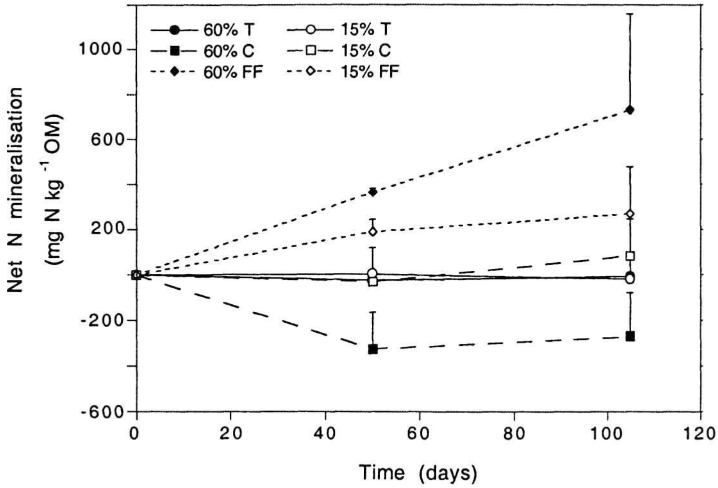


Figure 2. Accumulation of inorganic N (NH_4^+-N plus NO_3^--N) in materials from the top (T) and the centre (C) of wood ant nests and the forest floor (FF) outside the nests at Jädraås after 50 and 105 days at low (15% WHC) and high (60% WHC) moisture. Error bars indicate one SE. Negative values indicate net N immobilisation. OM organic matter.

C and N mineralisation in relation to the presence of conifer resin in ant nest materials (paper II)

Material and Methods

To test the hypothesis that resin acts as a fungicide and, thereby, reduces C and N mineralisation, two other incubation studies were carried out (paper II). In one experiment the F/H layer from a Scots pine stand was used and resin was added in amounts of 0%, 5% or 25% of the soil dry weight. In the other experiment, mixed litter from Scots pine and Norway spruce stands was used. Resin was added in amounts as above.

Results

Addition of resin to the F/H material resulted in an increase in fungal biomass, measured as ergosterol content. C mineralisation increased, while N mineralisation decreased (fig. 3). The addition of resin led to an immobilisation of inorganic N in fungal tissue (fig. 4). The addition of resin to litter materials did not significantly affect fungal biomass or C and N mineralisation. Consequently, we had to reject our initial hypothesis that, resin acts as a fungicide. Resin rather was a C-source that increased C mineralisation and decreased net N mineralisation in the F/H material. Because the initial stages of litter decomposition often are N limited, the addition of a C source to the litter strengthened the N limitation, which in turn had a neutral or negative effect on the fungal biomass and C mineralisation.

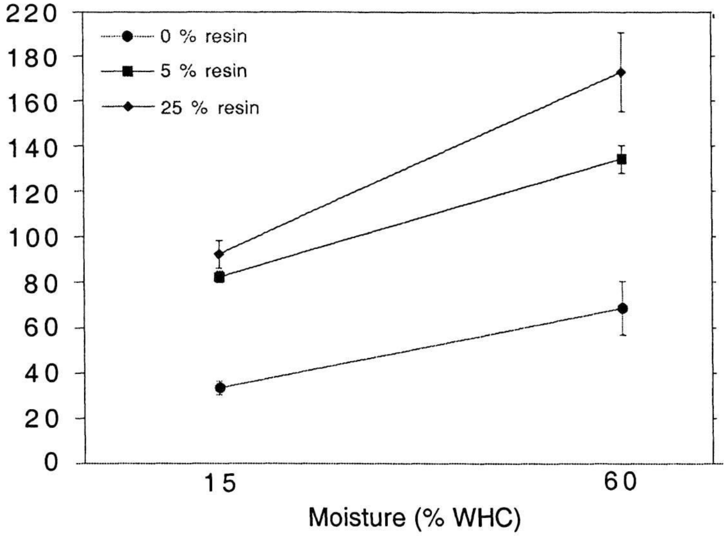


Figure 3. Cumulative CO_2 evolution (mg g^{-1} OM) during 105 days at high (60% WHC) and low (15% WHC) moisture. 0, 5 or 25% resin was added per unit weight of F/H layer dry matter, expressed per gram total OM (including resin). Bars indicate one SE.

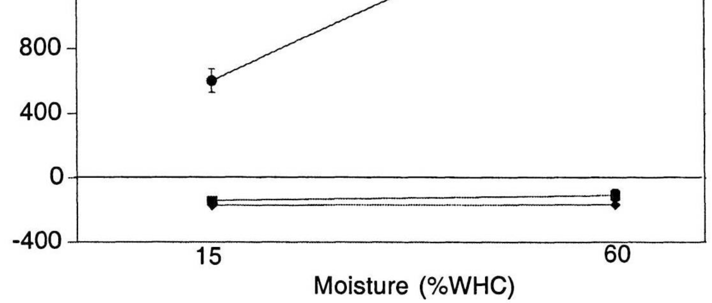


Figure 4. Net N mineralisation (µg g^{-1} OM) during 105 days at high (60% WHC) and low (15% WHC) moisture. For further explanation see fig. 3.

Effects of conifer resin and moisture levels on soil fauna (paper III)

Material and Methods

To investigate how the soil fauna might be affected by some of the specific features of the nest environment, we carried out another incubation study. We used mixed needle litter from Scots pine and Norway spruce, and the fresh material was treated as described as above. Resin was added to the litter material in amounts corresponding to 25% of the litter dry weight, a resin content commonly found in ant nests. In the control series, no resin was added. The soil moisture content was maintained at 60% WHC in one series and 15% WHC in the other series, corresponding to levels in moist litter and in dry ant nests, respectively. After 70 days of incubation, soil fauna was extracted using the Tullgren method. Oribatids, Collembola and Gamasids were determined to species.

Results

A principal component analysis showed that the moisture level was the most important factor affecting soil fauna composition in this experiment. A low moisture level had a negative effect on the abundance of oribatids, whereas the abundance of Collembola was negatively affected by the presence of resin (fig. 5). Correlations between Collembola and their predators, and between fungal biomass and fungivores, were usually insignificant. The study indicates that the abiotic conditions rather than the consumer-resource interactions are most important for the differences in faunal composition observed between ant nests and the litter layer in boreal forests.

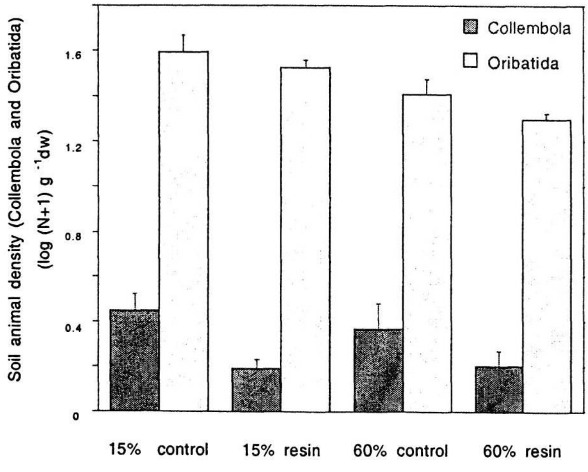


Figure 5. Mean densities of Collembola and Oribatida (log (n+1) g-1 dry wt soil, excluding resin) at low (15% WHC) and high (60% WHC) moisture levels in the control and resin treatments after 70 days of incubation. Error bars denote one SE.

Foraging behaviour of wood ants on the forest floor (paper IV)

Material and Methods

Wood ant foraging on the forest floor is seldom observed, but should be an alternative behaviour during periods of scarce food supply in the trees. To study the hunting behaviour of wood ants on soil invertebrates, ants were offered fly larvae (maggots) in two different quantities (6 or 2 per patch) at two distances from an ant trail. In another experiment, ants were offered minced tuna fish on the forest floor on both sides of the three main trails at 1, 3 and 5 m from these trails and at 10, 20, 30, 40 and 50 m from the anthills. The number of workers at each bait was counted after a fixed exposure period of 30 min on occasions from May 7 to September, 3, 1998.

Results

Maggots exposed on the forest floor were found by randomly patrolling ant scouts regardless of bait quality. However, scouts that found the baits with 6 larvae recruited workers faster and, on average, four times as many workers were recruited to the 6-larvae bait than to the 2-larvae bait. This indicates that ants can distinguish between poor and rich patches and that they are able to use this information to recruit more workers. Also, more workers were recruited and more maggots were carried away from patches nearby trails than from those far away On May 7, ants were found 40 m from the nests and 5 m from the trails. However, on May 21 the temperature was about 7 °C and only a few ants were exploring the forest floor. This day they stayed close to the nest and close to the trails. During the rest of the season, a large number of ants was found on the forest floor in the whole territory. The number of ants found at the baits was highest on June 25 (fig. 6). These results indicate that, during the warm season, ants explore and exhibit 'adaptive foraging behaviour' on the forest floor in the whole territory, not only close to trails. This means that ants have the potential to affect the abundance of soil animals in coniferous forests. Because ants feed on patches with the largest numbers or biomass of prey, ant predation has the potential to affect the diversity or composition of the soil fauna community.

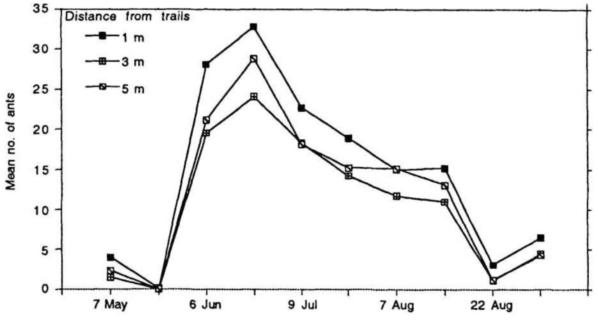


Figure 6. Temporal dynamics of wood ant behaviour on tuna fish baits after 1 h of exposure at different distances from the ant trails (1, 3 and 5 m) on different occasions (May 7 to September 3).

Effect of ants as consumers on soil fauna (papers V-VII)

Introduction

It has been suggested that ants are important top predators in the soil food web (Bengtsson et al., 1995). To investigate if ants indeed affect the abundance and composition of soil fauna by predating, interfering or competing with them, three different experiments were carried out in the field. In one study, I investigated the soil fauna of a pine-dominated forest with a few ant territories, separated from each other by areas lacking wood ants (a natural experiment, paper V). In another study, a field experiment was carried out during a four-year period on the impact of wood ants on the abundance and composition of soil fauna by excluding ants from small areas inside their territory (paper VI). In both studies (paper V and VI), I hypthesised that the abundance of larger soil fauna, i.e, Araneae, Coleoptera and Diptera larvae would be negatively affected by the presence of ants. Because of competion with or intra-guild predation by ants on other larger predators, effects on smaller-sized soil fauna, that are prey of both groups, were expected to be difficult to detect.

Ant predation may become heavier on the forest floor than in the tree canopy if the biomass of arthropods in the trees temporarily becomes low, for example during periods of severe fluctuations in precipitation or unfavourable temperature. Hence ants may have a temporary but sometimes important effect on the soil fauna. In the last study, I tested this idea (paper VII). I increased the density of wood ants on the forest floor by prohibiting ant access to the trees. The foraging behaviour of ants as well as their effect on soil fauna was investigated. I hypothesised that ants by forced to forage on the forest floor will affect soil organisms to a larger extent than under normal conditions.

Effect of wood ants on the soil fauna in a coniferous forest (paper V)

Material and methods

The study site Blåhult (Hökensås) is dominated by Scots pine (*Pinus sylvestris* L.), and only scattered individuals of Norway spruce (*Picea abies* (L.) Karst.) and silver birch (*Betula pendula* Roth.) can be found. The ground vegetation is very homogenous and consists mainly of mosses, reindeer lichens and the dwarf-shrubs *Vaccinium vitis-idaea* and *V. myrtillus*. The area harbours a sparse population of wood ants, but the presence of a large number of dead anthills shows that in the past the wood ant population was dense. Many of these ant colonies died in the seventies. After the seventies, the remaining active anthills occur near spruce or birch trees in this area producing a natural experiment on wood ant impacts. Three pairs of ant-rich and, directly adjacent, ant-free areas (block) were selected and compared with regard to the soil fauna.

Results

The densities of Protura, Heteroptera, Diptera larvae, Coleoptera and Araneae did not differ between ant-free areas and areas where ants were present. To compare the impact of ants with the impact of differences in vegetation on soil fauna, a partial redundancy analysis (RDA) was carried out. The proportion of the variation in soil fauna composition among the 36 sub-samples that could be attributed to differences in vegetation was larger than the proportion explained by the presence or absence of ants (32 vs. 11% in a partial RDA; L. Lenoir, unpublished data; fig. 7.)

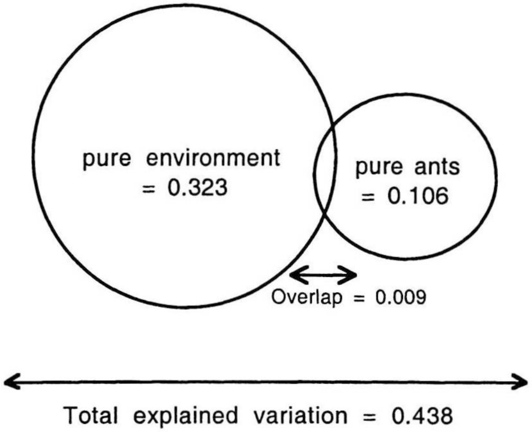


Figure 7. The proportion of explained variation in soil fauna by ants and by environmental factors, analysed by partial redundancy analysis. Environmental factors included soil moisture and composition of the ground vegetation.

Excluding of wood ants in a long term experiment and their effects on soil fauna (paper VI)

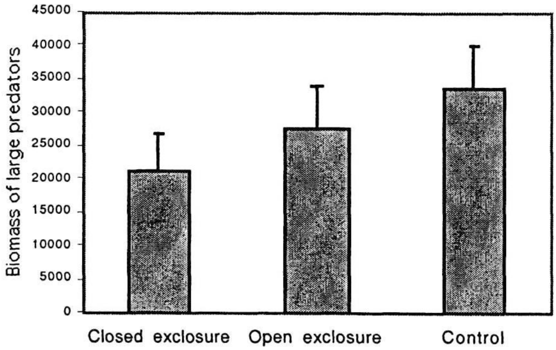
Material and Methods

The impact of a super-colony of wood ants on the abundances of various soil faunal groups (e.g. Oribatids, Collembola, predatory Coleoptera, Diptera larvae, Araneae, earthworms) was studied in a mixed forest during a four-year period. Inside the ant territories, ant-free areas were created by digging down five fences. The fences had a diameter of 1.30 m. Five other fences (open fences), each with an open entrance for ants (10 cm high, 10 cm broad), were placed at about 5 m distance from the other closed fences. Near these two types of exclosures, open control plots were selected. Soil samples of 100 cm^{-2} were taken three times a year, in 1997, 1998 and 1999 and two times in 2000. Soil fauna was extracted by using Tullgren funnels. Biomass of the fauna was calculated by multiplying individual numbers by dry masses acquired from the literature. The soil fauna data was statistically analysed by repeated measurement methods. At the last sampling occasion, in July 2000, all litter material in the fences and control plots was collected and the soil fauna was extracted. The data was analysed by paired t-tests.

Results

Repeated measurement analyses did not reveal any effect of ants on the abundance of any of the components of the soil fauna community or their biomasses. However, the treatment had an effect on the soil fauna on some separate sampling occasions. On the last sampling occasion, the abundance of spiders, predatory beetles and the total number of large predators was larger in the control plots than in the closed fences. These results should be interpreted as 'fence effects'. No differences were found between the two types of exclosures, although the total numbers of large predators tended to be lower in the closed than in the open exclosures (fig. 8). No effects of ants on the faunal biomass were found. The results indicate that wood ants have only minor effects on soil fauna and that these effects are very variable over time. They also suggest that the spatial scale of the experiment was too small, and that examinations of ant effects on soil fauna require studies on larger scales (e.g. paper V).

(A)



(B)

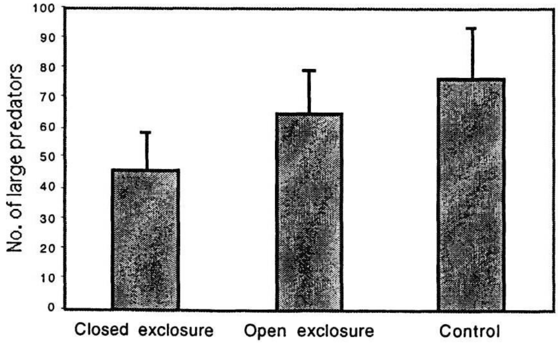


Figure 8. Mean number m^{-2} (A) and total biomass m^{-2} (B) (±SE) of predators larger than µg dry body wt, collected on the last sampling occasion, July 2000, in the two types of exclosures and control plots.

Behaviour of ants when excluded from trees and their effect on soil fauna (paper VII)

Material and Methods

To examine the foraging behaviour of wood ants on the forest floor, and the impact on soil fauna of increased numbers of wood ants on the forest floor I carried out a field experiment.. The study was conducted during the spring and summer of 1999 in the Lunsen forest near Uppsala. Lunsen is a mixed forest dominated by Norway spruce (*Picea abies* (L.) Karst.), Scots pine (*Pinus sylvestris* L.), birch (*Betula* spp.) and aspen (*Populus tremula* L.), and with other deciduous trees at a low density. Three pairs of anthills, each pair similar in terms of size of the nests and territories as well as in composition and structure of the vegetation in the territories, were selected. For each pair of anthills, one control territory (control plot) was randomly chosen. In the other territory (treatment plot), the ants were prevented from foraging in the trees with the intention to increase ant activity on the forest floor. However, the immediate response of the ants was to increase their foraging area. Therefore, the treatment was gradually expanded following the increase in area of activity of the ants. During the summer, the activity of ants was estimated by determining the number of trees with foraging ants (treated trees included in the treatment plots) and by counting the numbers of ants going to and from their nests. The number of prey items and nest materials carried by the ants to the nests was counted on every trail during 5 min. on May 19, May 27, June 29 and July 19. Prey items were, if possible, determined to the genus level and registered as 'soil-living fauna', 'tree-living fauna' or ‘unidentified prey’. To investigate the effect of the treatment on the soil fauna, pitfall traps were placed in the treated and control plots. The traps were in operation during May 17-28, June 20-July 1, July 8-29 and August 12-23. Collembola found in the traps were determined to species. Opiliones, Lumbricidae, snails, slugs, Diplopoda and Diptera larvae were not determined any further. Spiders and beetles were determined to families and classified into 11 size groups of <1 mm, 1-2 mm, 2-3 mm, etc. up to >10 mm length. Savolainen (1991) found that about 50% of all prey collected by *F. polyctena* was between 3 and 5 mm large. Therefore, spiders and beetles were also classified into three categories: <3 mm, 3-5 mm and >5 mm. The number of spider webs was estimated by visual counting in 10 randomly distributed 0.5 x 0.5 m quadrats in each plot, on May 28, July 1, July 28 and August 23. In each plot, six soil samples of 100 cm^2 were taken on August 19 and soil animals were extracted in Tullgren funnels. The extracted animals were determined to species.

Results

When excluded from trees, ants changed their foraging behaviour by searching other trees further away from the nests rather than searching more intensively for prey on the forest floor (fig. 9). Contrary to my initial hypothesis, the number of preys caught by ants were higher in the control plots than in the plots where the trees were not accessible to the ants. Also the proportion of soil-living to tree-living prey tended to be higher in the control plots. No obvious effect of the treatment on the abundance of major faunal taxa trapped in the pitfalls was found. No treatment effect on the composition of Coleoptera or Araneae families was found. Further, no effect on the abundance of Coleoptera families was found. Nor was there any significant treatment effect on any of the size classes of the Coleoptera or Araneae on

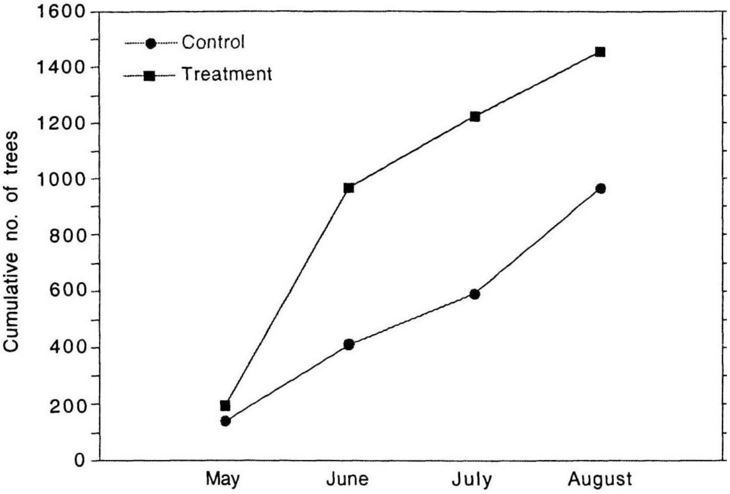


Figure 9. Cumulative number of trees visited by ants in the control and treated (no access to the canopy) plots during the experimental period. Mean of three pairs of territories. In treated territories, trees from which ants were excluded are included.

any sampling occasion. However, in the treated plots, less Linyphiidae spiders were caught in the pitfall traps than in the control plots. The number of spider webs was not affected by the treatment. This indicates that ants had a negative effect on the activity of Linyphiids but these spiders can escape from interference with ants by 'staying by their webs'.

Discussion

Impact of wood ant nests on the forest soil environment

Results from studies on the effect of ants on physical and chemical soil properties, for instance, on particle size distribution, soil organic matter, bulk density and nutrients, are variable and contradictory (Lobry de Bruyn and Conacher, 1990; Hulugalle, 1995). This has been explained by the soil differences in various habitats (Lockaby and Adams, 1985; Hulugalle, 1995; Whitford and DiMarco, 1995; paper I), differences in behaviour of different species of ants (Whitford and DiMarco, 1995), and the size of ant colonies (Petal, 1998). In most studies, comparisons have been made between ant nest material and surrounding soil. However, the surrounding soil may have been affected by ants in the past. and thus, it cannot be considered as a pure control (Lobry de Bruyn and Conacher, 1990). Ants are believed to affect the entire soil profile in a couple of hundred years (Lal, 1988; Eldridge and Pickard, 1994). Also, the large variability in the amount of inorganic N in individual ant nests and between soil samples (paper I) can obscure comparisons between ant nest materials and surrounding soils. Nevertheless, the results on nitrogen content and pH presented in paper I indicate that these nest properties were mostly dependent on the litter quality, whereas the properties of the forest floor were dependent on both litter quality and mineralogy. Thus, ants will reduce the influence of the underlying soil by concentrating litter material in heaps. It is clear that the chemical properties of wood ant nests differ from the surrounding soil, and the nests are likely to increase spatial heterogeneity of the forest floor. Lee and Foster (1991) indicated that effects of ants on soil structure are generally concentrated in small areas around nests. Hence ants do not affect soils on a large scale as the non-social, dispersed populations of earthworms.

Wood ants may favour different plant and fauna species on or in their nests than what usually is found in the surroundings. Hence, wood ant nests contribute to the soil heterogeneity in the forest, and thus, ants might contribute to increasing local biodiversity in forest ecosystems. Laakso and Setälä (1998) compared the fauna living inside nests of *F. aquilonia* with the fauna in the surrounding soil and found that the nest inhabitants, including earthworms, could be classified into two distinct categories: soil specialists and ant nest specialists. Very few species were common in both habitats. They also found that, relative to other groups, oribatid mites were more common in ant nests than in the surrounding soil. They stated that the abundance of nest specialists is important for species richness of the forest floor. Ant nests covered only a very small part of the whole study area but harboured many soil fauna species that are rare in the adjacent soil.

In paper III, I wanted to examine some of the factors that may have an effect on the abundance and composition of soil fauna in ant nests. Moisture was especially important for the total numbers of Oribatida and the oribatid species composition. High moisture level seemed to depress the abundance of oribatids. Brachychthoniidae were considered to be nest specialists by Laakso and Setälä (1998). Our results suggest that Brachychthoniidae are common in ant nests because of their tolerance to a dry environment. Another possible explanation for the low numbers of Oribatida at 60% WHC in our experiment is that the life processes were accelerated at this moisture level due to a good food supply and that a large number of Oribatida had terminated their life cycle and died before sampling. We only carried out a short-term experiment (70 days), and did not investigate the effect of low moisture on life-history traits of Oribatida. Therefore, this suggestion remains to be conclusively examined. Few Collembola seem to be true ant-nest specialists (Laakso and Setälä, 1998). This low abundance could be explained by several factors: low moisture inside the nests, presence of earthworms, the quality (high C/N ratio) of the nest material, or resin content as suggested by our study.

Resin might also affect the composition of plant species growing on mounds of wood ants. The incubation study showed that addition of resin to F/H layer material led to an immobilisation of inorganic N (paper II). A lack of inorganic N will prevent plant roots to establish in the ant nest. However, some plant species like *Vaccinium vitis-idaea* and *V. myrtillus* are able to take up organic N through their ericoid mycorrhiza (Read, 1991; Näsholm et al., 1998). These species are commonly observed growing on the slopes of ant mounds in the boreal forest.

Impact of wood ants on the soil food web

The field studies suggested that the impact of ants on the soil food web is small and that the proposition that ants can have large effects on soil fauna and are acting as key-stone species with regard to the soil faunal community (Bengtsson et al. 1995) has to be rejected. It has been suggested that ants are adapted to search for food in the canopy (Skinner 1980, Skinner and Whittaker, 1981; Laakso and Setälä 2000), where they indeed can affect the arthropod community (e.g. Haemig, 1994; Halaj et al., 1997; Karhu, 1998). Brüning (1991) observed that *F. polyctena* has very poor ability to detect agile potential prey. Many observations demonstrated that ants did not recognise spiders as potential prey when they sat still in their webs (Brüning, 1991). *Formica* spp. often overlooked immobile prey, even in the canopy (Hassell and Southwood, 1978; but see Paper IV). Moving spiders, if noticed and attacked by ants, had no difficulties in escaping, because the ants were unable to trail the escaping spiders, but searched for them at random in various directions (Brüning, 1991). However, in paper IV, I showed that ants can forage on the forest floor in their whole territory on mobile and immobile prey and that they even can adapt their forage activity to the amount of prey available. This indicates that ants might have the potential to affect and regulate soil fauna.

There are two main explanations why researchers have not been successful in shedding light on the possible effects of ants on other soil animals. The first explanation has to do with the heterogeneity of the forest soil and the complexity of the biological interactions between soil invertebrates. The other explanation is has to do with the behaviour of ants and their requirements to sustain their population.

Heterogeneity of the forest and complexity of biological interactions

Natural soil heterogeneity in the field is often large and there is large variation in abundance and composition of soil fauna caused by other factors than ants. Therefore, the impact of ants is often likely to be small and difficult to detect (paper V). Due to the non-random selection of nest site and trail location by ants (Laine and Niemelä 1989), it is difficult to find matching sites with and without ants. Restricted possibilities for replication of both ant-poor and ant-rich sites have often been a shortcoming in field studies or in natural experiments considering ants. Therefore, the differences between ant-rich and ant-poor areas found by some authors, can reflect differences in vegetation, soil conditions or sun-exposure between these areas rather than differences in ant activity. Cherix and Bourne (1980) found that some species of spiders were more abundant inside the ant territory, while other species were more common outside the territory. They suggested that this was due to differences in the structure of vegetation and humidity between the two areas. Sudd and Lodhi (1981) found that Acarina and Sminthuridae were more abundant inside a wood ant territory than outside. It was suggested that these differences were caused by differences in soil or litter conditions. Oliver and Beattie (1996) found a negative correlation between ant and beetle richness. They suggested that this might be a result of different habitat demands for the two fauna groups. Ants were uncommon in forests with a closed canopy and a high soil moisture level, while beetles were both common and species-rich in these forests. In contrast, in forests with an open canopy and low moisture the reverse was true.

An alternative approach to investigate effects of wood ants is to remove whole ant nests from a site (Laakso and Setälä, 2000) or to exclude or reduce ants from small plots inside the territory (paper VI; Laakso and Setälä 1998). In the study presented in paper VI, I used fenced plots to exclude ants from small parts of the forest floor. Fenced plots are usually small in relation to the size of the natural habitat of the organisms concerned. For many organisms it is not known how a reduced habitat size and restricted migration possibilities will affect, e.g., interspecific competion (Petersen and Hastings, 2001). Fenced plots as small as 1 m^2 were suggested to be adequate for studying competion between young Lycosidae spiders, but these plots are far too small for, e.g., a long-term study of predation by adult wolf spiders (Wise, 1993). For long-term studies on spiders, exclosures of at least one order of magnitude larger in area are recommended (Wise, 1993). The differences between the closed fences and the control plots, as found for the abundance of spiders in 1997, should be interpreted as 'fence-effects'. At the last sampling occasion in 2000, the control plot harboured more spiders and predatory beetles than the closed exclosure, indicating that these large predators were negatively affected by the barrier and that the small local populations went extinct when they no longer received immigrants from the outside. For predatory beetles, this might be surprising, because the adult forms can fly, and thus enter the closed exclosures. Even spiders can migrate through the air and one would expect that ant-free spots within a wood ant territory could act as refugia for other predators. My results suggest that this was not the case, and the barriers made it less likely that the exclosures received immigrants. Species at higher trophic levels are more likely to have large home ranges and their dynamics depend on landscape composition at larger scales than local patches (Bengtsson et al. subm.). Although it has never been tested, it is often thought that larger enclosures contain and sustain more ecological complexity, e.g. more possibilities for environmental heterogeneity and more biotic interactions (Naeem, 2001).

There are some other explanations for the rarity of observed ant-induced effects on soil fauna. Interference of ants with other insect predators (Gridina, 1990), and the competition for food with wood ants (Aho, 1997 cit. in Laakso and Setälä, 1998) can force other predators to forage in habitats with lower wood ant density and, hence, compensate for changes in wood ant density. Thus the total predation pressure by macro-arthropod predators on soil animals is only slightly or not at all affected by the variation in ant activity or abundance. Another factor that might diminish the effects of ants on soil fauna is the high number of alternative prey and predator species. Also anti-predatory adaptations and the complex spatial structure of the soil offering refugia strongly decrease the potential of individual predator species to influence the invertebrate community in the boreal forest floor and vegetation (Laakso and Setälä, 2000).

The behaviour of ants

Ant densities are not easy to manipulate. Wood ants live with a great number of co-operating individuals in large nests, often in super-colonies (*F. polyctena* and *F. aquilonia*). The radius of the territory of a single ant nest may over reach 50 m (Laakso and Setälä, 1998) or even up to 80-100 m

(Brüning, 1991; Savolainen, 1991). Nests may split, secondary and seasonal nests might get established and nests might get abandoned for known or unknown reasons. It is possible to introduce wood ant nests in wood ant-free forests (Fanfani, 1979), but it will not be possible to manipulate the number of active workers or the range of the territory in a consistent way.

In one study (paper VII) I tried to increase the foraging activity of ants on the forest floor within their territory by excluding them from trees. Ants, when excluded from trees, tended to move over larger distances from the nests, tried to explore more trees, and were less efficient in catching prey. The results suggest that ants, when cut off from trees, try to find other trees further away from the nests rather than changing their foraging behaviour.

In natural experiments, the effects of introduced wood ants (*F. lugubris*) on the native ant population in Canada have been investigated (Finnegan, 1975) as well as effects of other ant species that were introduced or invaded in new areas. Wood ants have been introduced to forests to control forest pests (Fanfani, 1979; Pavan, 1979), but the effect on soil fauna other than ants has not been investigated. Unfortunately, the opportunities to study effects initiated by natural experiments are often poorly utilised (Diamond, 1986). This was also the case with the Hökensås area (paper V). Nothing is known about the possible initial effects of ants on soil fauna after the perturbation or the trajectories of the communities over time. However, thirty years after the disturbance took place only a very small effect of ants on the abundance or composition of soil fauna could be found.

An alternative way to study the effect of wood ants on soil fauna could be to investigate soil fauna on islands with and without ants. Nilsson et al. (1988) showed that islands, where wood ants were common, there was a relatively low species richness of carabids and snails. The strength of this type of natural experiment is that it is possible to investigate on a large spatial scale the long-term effects of ants in the ecosystem, but it requires that islands are well matched with respect to other environmental factors.

Conclusions

The incubation studies (paper I and II) showed that wood ants can be considered as ecosystem engineers. The nests, built and maintained by the ants, are important habitats for an ant-specific flora and fauna, thus increasing the biodiversity of the forest. The study on anthill materials from Jädraås and Sunnersta (paper I) showed that the chemical properties of *Formica* ant nests differ from the surrounding soil, and the nests are likely to increase spatial heterogeneity of the forest floor. Anthill properties are mostly dependent on the litter quality, whereas soil properties are dependent on both litter quality and mineralogy. The results of the incubation study with resin (paper II) indicate that resin acts as a carbon source that increases C mineralisation (mainly from the resin itself) and decreases net N mineralisation. The latter factor might be important in preventing plants dependent on inorganic N from invading and covering the ant mounds. However, some plants like *Vaccinium vitis-idaea* and *V. myrtillus* are able to take up organic N through their ericoid mycorrhiza. These species are often the only vascular plants that are commonly observed growing on the slopes of the ant mounds in the boreal forest. It is possible that ants can influence which plant species will grow on the nests by collecting seeds and resin (paper II). The dry conditions in the ant nests and the addition of resin to the nest material might also determine the composition of soil fauna living in the nests. In our study (paper III), Collembola were negatively affected by resin, while oribatids seemed to be resistant to low moisture conditions.

Wood ants can forage on the forest floor during a large part of their active season (paper IV). This means that ants have a potential to affect the abundance of soil animals in coniferous forests. Because ants feed on patches with the largest number or biomass of prey, ant predation has the potential to affect the diversity or composition of the soil fauna community.

However, I found little evidence supporting the hypothesis that wood ants have a large impact on the abundance or composition of the soil fauna (papers V-VII). Neither in a natural experiment (paper V), nor in the experimental attemps to exclude ants (paper VI) or increase ant activity on the forest floor (paper VII), did ants have more than a very minor effect on the soil fauna community. Nevertheless, due the problems involved in doing experiments at the larger scales at which ants may be important, it might be too early to rule out the proposition that ants at least sometimes are acting as a key-stone species with regard to the soil faunal community. The proper test of this hypothesis requires new natural experiments in which the response of soil fauna on the increase or decrease of wood ant activity will be studied during a long time period. Also investigations of soil fauna on islands with and without wood ants may be a possible alternative to study the impact of wood ants on the soil fauna community. This could occupy at least one more enthusiastic PhD-student for several years!

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