Ann. Zool. Fennici 37: 93–100 ISSN 0003-455X
Helsinki 29 June 2000

Impacts of wood ants (*Formica aquilonia* Yarr.) on the invertebrate food web of the boreal forest floor

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Received 6 March 2000, accepted 19 March 2000

Laakso, J. & Setälä, H. 2000: Impacts of wood ants (*Formica aquilonia* Yarr.) on the invertebrate food web of the boreal forest floor. — *Ann. Zool. Fennici* 37: 93–100.

We studied the impact of wood ants on the structure and functioning of the invertebrate food web of boreal forest during a three-year period. Special emphasis was put on the detritus-based food web. The density of wood ants was reduced > 90% by eliminating whole wood ant colonies from five areas in Central Finland, and leaving five areas as controls. We monitored the growth of spruce, pine and birch seedlings planted on homogenised plots, and development of the invertebrate community in soil and vegetation. The ant removal had little effects on the structure of the invertebrate food web. However, biomasses of predators caught in pitfall traps were 60% smaller under high ant density than under low ant density. Also, at the end of the experiment the biomass of the lumbricid earthworm *Dendrobaena octaedra* was reduced by 54% in the homogenised plots without ant nests. Removal of wood ants had no influence on soil microbial biomass, concentration of soil mineral nitrogen, plant N uptake, or plant growth.

1. Introduction

Wood ants are commonly considered as a keystone taxon in temperate and boreal forest ecosystems due to their exceptionally high abundance, metabolic activity, and diverse role in community and ecosystem processes (e.g. Laine & Niemelä 1980, Pokarzhevskij 1981, Fowler & Macgarvin 1985, Hölldobler & Wilson 1990, Rosengren & Sundström 1991, Whittaker 1991, Froutz *et al.* 1997). Besides preying upon fauna at several trophic positions (e.g. Skinner 1980, Skinner & Whittaker 1981), wood ants obtain a significant part of their nutrition by feeding on honeydew excreted by aphids (e.g. Skinner 1980, Rosengren & Sundström 1991). The polyphagous feeding habits of the wood ants ensure the maintenance of a large and stable biomass, which is likely to increase the potential of the ants to efficiently control their prey.

The importance of top-down forces and omnivorous predators in structuring communities has long been debated. The role of predatory interactions and their indirect consequences in producing trophic cascades are often emphasised (Paine 1966, Oksanen *et al.* 1981, Carpenter *et al.* 1985).

Recent syntheses, however, suggest that food webs are often more complex, and omnivory is more common than previously thought, which hinders the occurrence of trophic cascades (Polis 1991, Polis & Strong 1996). Moreover, the traditional view according to which omnivores are not only rare but decrease community stability (Pimm 1982), has been challenged by the recent empirical and theoretical findings (e.g. Polis 1991, Fagan 1997). Wood ants as abundant omnivores inhabiting species-rich food webs are therefore a useful tool to assess the importance of omnivorous predators in the organisation of food webs.

The impact of wood ants on ecosystem-level phenomena, such as primary production and nutrient cycling has predominantly been studied in two distinct habitats, tree canopies (Laine & Niemelä 1980, Mahdi & Whittaker 1993) and in nest mounds of wood ants (Pokarzhevskij 1981, Froutz *et al.* 1997, Laakso & Setälä 1998), while the forest floor has received little attention. Scattered data from the latter habitat indicate, however, that wood ants can affect the structure of soil food webs. For example, wood ants are shown to have a negative association with soil inhabiting arthropod predators (Cherix & Bourne 1980, Niemelä *et al.* 1992, Laakso 1999) and microbivorous soil fauna (Rosengren & Sundström 1991), and a positive association with earthworms (Laakso & Setälä 1997, Laakso 1999), which have a potential to indirectly control the rate of various soil processes (e.g. Swift *et al.* 1979). However, as the available data on the ant-induced effects on soil food webs are mainly correlative, it remains unclear whether the observed correlations are due to other confounding factors, such as non-random selection of nest site and trail location by the ants (Rosengren 1971, Laine & Niemelä 1989).

In this paper, we investigate whether wood ants are a keystone species (for definition *see* Bond 1994) in the boreal forest floor. To overcome the inherent difficulties resulting from the interpretation of correlative data, or the use of fences that can prevent movements of non-target fauna, we manipulated wood ant density by eliminating whole ant colonies. The consequences of ant exclusion on invertebrate community structure, nitrogen mineralisation, and growth of spruce, pine and birch seedlings were monitored during three growing periods.

We hypothesised the removal of wood ants to result in considerable direct and indirect changes in a food web, which may also reflect to ecosystem processes. Specifically, we expected the removal of wood ants to have a negative effect on nutrient cycling and plant growth due to the positive association of ants with earthworms (Laakso & Setälä 1997, 1998), and the direct positive influence on nutrient flows (Oinonen 1956, Pokarzhevskij 1981, White 1985, Froutz *et al.* 1997).

2. Material and methods

2.1. Establishment of the experiment

Ten medium-sized ant nest territories sharing a similar field and canopy layer vegetation were selected for the experiment. The study site in Konnevesi, Central Finland (62°37´N, 26°20´E), is a seven hectare forest area surrounded by a clear-cutting and a lake. The site is dominated by mature Norway spruce (*Picea abies*), silver birch (*Betula pendula*) and Scots pine (*Pinus sylvestris*), and harbours on average nine *Formica aquilonia* nest mounds per hectare.

Five territories were randomly selected for a treatment with reduced ant density, the rest remaining as control colonies with normal ant density. Ant density was reduced in the five territories in July 1994 by mechanically removing the ant nest mounds. The ants escaping this procedure were caught by fencing the nest remains for two months using plastic walls that had openings with pitfall traps for the ants. Ant nest mounds in the adjacent territories were mechanically removed to prevent ants from invading from the surroundings. Restoration of the removed nests, and build-up of new satellite nests were prevented by removing the new nests, applying 1% water solution of the insecticide Foxim® (Foxim® is specifically designed to kill ants and disappears in 2–3 weeks from the soil) on the nest remains during the summer and autumn of 1994. To avoid the effects of Foxim® on non-target fauna, only the mechanical removal procedure was applied inside the experimental territories (radius approximately 20 m).

To increase accuracy of measurements, vegetation, soil organic matter, and roots growing in mineral soil at < 25 cm depth were removed from two circular 0.44 m^2 patches located three meters from each nest, the distance between the two patches being 4–6 m. A new soil profile with a homogenised 2.3 cm thick layer of raw humus and 1.1 cm layer of mixed litter was established on the mineral soil on 21 July. Two 1.5 year old birch (*Betula pendula*, height ranging 45–65 cm), spruce (*Picea abies*, height 43–60 cm), and pine (*Pinus sylvestris*, height 33–40 cm) seedlings grown in a tree nursery were planted on each of the homogenised plots to monitor the ant-induced effects on plant growth, survival, and nutrient uptake.

2.2. Measurements

2.2.1. Animal community and trophic structure

Soil microfauna and mesofauna, and insects on the tree seedlings were sampled five times from August 1994 to August 1996 in the patches. The sample size for microfauna (Nematoda and Tardigrada) was 3 × 1 cm^2 (the fauna was extracted with the wet funnel technique by Sohlenius (1979)), 3 × 10 cm^2 for microarthropods (modified MacFadyen high-gradient extraction), 3 × 25 cm^2 for enchytraeids (wet funnel extraction; O'Connor 1962). Insects (including ants) on tree seedlings were counted at the site without removing the specimens. The number of wood ants on the litter layer of the plot was counted using the same method. At the destructive sampling at the end of the experiment micro- and mesofauna samples were also taken from the patch surroundings and 50% of the patch organic matter was used for extracting lumbricids (wet extraction; Huhta & Koskenniemi 1975). Only soil organic layer (litter + humus) was sampled.

A sample (227 cm^2 and 4 cm thick) for soil macroarthropods and lumbricids was taken in the vicinity of the plots five times during 1994 and 1996. In June and August 1996, macroarthropods were sampled at three additional locations within the territories: two pitfall traps placed inside each of the patches for five days, and 25 hits with a sweep-net per patch surroundings for both field and canopy (maximum height < 2.5 m) layer vegetation.

Meso- and macrofauna were identified mainly to species or genera (taxonomic resolution depending primarily on the developmental stage of a specimen), and microfauna to order (Nematoda/Tardigrada). For the trophic structure analysis, the taxa were grouped into ten trophic groups: (1) small (body mass < 5 µg d.m.), (2) medium (< 5–500 µg d.m.) and (3) large microbi-detritivores (> 500 µg d.m.), (4) small and (5) large omnivores, (6) micro-, (7) meso- and (8) macrofauna predators, (9) herbivores, and (10) Nematoda and Tardigrada as small "miscellaneous feeders" with uncertain nutritional status. The trophic grouping was based on feeding preferences obtained from the literature (meso- and macrofauna: Luxton 1972, Persson *et al.* 1980, Karg 1986, Werner & Dindal 1987, Walter *et al.* 1988, Koch 1989a, 1989b, Ponge 1991, Siepel & de Ruiter-Dijkman 1993, Palm 1996). Biomasses were estimated by multiplying individual numbers of a taxon or a size class with measured dry masses (10 h at +75 °C), or masses acquired from the literature (microarthropods: Huhta *et al.* (1975), macroarthropods: Persson *et al.* (1980), Sample *et al.* 1993). Complete lists of parameters used to calculate the biomasses of taxa and trophic groups are available at http://sekj.pc.helsinki.fi/.

2.2.2. Plants, microbes and abiotic variables

Plant height, a three level index for plant survival (live, suffering, or dead individual), damage caused by herbivores (for the birch only; three intensity levels based on the amount of leaf area eaten by herbivores), soil mineral nitrogen content (2M KCl extractable NH_4^+ and NO_3^-), and pH (water) were measured twice a year (6 July and 28 August) between August 1994 and August 1996 from the homogenised plots.

At the end of the experiment the homogenised plots were destructively sampled for plant above ground biomass, and contents of total C, N, and S in the spruce seedlings. Soil dry matter content (24 h at +80 °C), loss on ignition (5 h at +550 °C), pH (H_2O), microbial respiration (at 22 °C using an IR carbon analyser) and biomass (SIR method: glucose concentration of 20 mg ml^{-1} soil water, soil humidity 60% of WHC, biomass-C calculated according to Anderson and Domsch 1978) were measured from the soil both inside and outside the plots.

2.3. Statistical analyses

Estimates of the variables were averaged within each of the territories, which formed 5 + 5 independent observations. Repeated ANOVA (ANOVAR) or Student's *t*-test was applied for the functional variables (e.g. plant biomass, soil chemical properties, and microbial respiration) and for the animal species and trophic groups with a large contribution to the community biomass. Changes in animal community and trophic structure were tested with a Canonical Correspondence Analysis (CCA) using the Canonical Community Ordination program (CANOCO; Ter Braak 1987). A Monte Carlo permutation (999 permutations) was used to test statistically whether the communities were significantly related to the ant removal that was treated as a nominal environmental variable. The effect of time was removed by setting the five sampling times as nominal covariables, and using a restricted Monte Carlo permutation for repeated measurements (provided by CANOCO v. 3.1). Separate ordinations and permutation tests were carried out for samplings (1) in the plot (soil fauna + fauna on the seedlings; total 99 taxa), (2) pitfall trappings (63 taxa), (3) soil fauna outside the plot (79 taxa), and sweep-net samplings in (4) the field (46 taxa), and in (5) the canopy layer (99 taxa).

3. Results

Removal of the ant nests was accompanied with a 91%, 96% and 90% reduction in ant density in the homogenised plots (both plants and the plot surface; mean of intact treatment 62 ind. m^{-2}, F = 22.7, P = 0.001), in the litter surrounding the plot (mean 45 ind. m^{-2}, F = 40.1, P < 0.001), and in the field and canopy layer vegetation (mean 21 ind. per 25 sweeps, F = 23.3, P = 0.001), respectively. Ant density showed strong seasonal fluctuations (F = 22.7, P = 0.001, F = 40.1, P < 0.001, F = 23.3, P = 0.001 for time, and F = 1.6, P = 0.20, F = 3.5, P = 0.018, F = 80, P < 0.001 for time X ant density in homogenised plots, litter layer, and vegetation, respectively) and remained always higher in the control territories than in the territories without ant nest mounds.

Abiotic conditions, such as soil moisture, ash content, pH, and the amount of photosynthetically active radiation (mean = 268, S.E. = 54 µE m^{-2}) in the homogenised plots and in the surrounding soil remained similar between the ant density treatments throughout the experiment. At the destructive sampling the homogenised plots had higher pH, ash, and dry matter content than the surrounding soil (mean ± S.E. pH: 4.75 ± 0.05 and 4.17 ± 0.05; ash content: 0.46 ± 0.01 and 0.29 ± 0.06; dry matter content: 0.65 ± 0.03 and 0.56 ± 0.03 for homogenised plots and the surrounding soil, respectively).

3.2. Community and trophic structure

CCA-analyses performed separately for the five samplings (see methods) revealed that both the species composition and the trophic structure of the communities varied in time (CCA analysis in which the five sampling times were considered as environmental variables; results not shown). However, CCA analysis showed no differences in species or trophic group composition in any of the five sub-communities despite the over 90% reduction in *F. aquilonia* density (CCA analysis in which the temporal variation was removed; F < 1.6, P > 0.11 for all samplings, 999 permutations). Nevertheless, univariate tests of the data from the pitfall traps suggest that ant density affected the activity of invertebrate predators (pitfall traps are considered to measure mainly the amount of actively moving fauna; *see* Niemelä *et al.* 1992) in the homogenised plots: biomasses of predators belonging to mesofauna (body mass 5–500 µg d.m.; F = 14.3, P = 0.005) and macrofauna (> 500 µg d.m.; F = 19.0, P = 0.002) in the pitfall traps were on average 67% and 60% smaller in the high ant density treatment than in the low ant density treatment, respectively (Fig. 1). Also, at the destructive sampling the biomass of the lumbricid *Dendrobaena octaedra* was 54% smaller in the homogenised plots with low ant density (128 ± 15 mg d.m. m^{-2}) than in patches with normal ant density (280 ± 49 mg d.m. m^{-2}, Student's t = 3.0, P = 0.017). Other trophic groups or dominant taxa did not respond to reduction in wood ant density (results not shown).

The ant density had no effect on microbial respiration or on biomass. At the destructive sampling the mean microbial respiration was 33.5 ± 1.5 and 65.9 ± 5.5 µg CO_2-C h^{-1} g^{-1} d. m. soil, and microbial biomass 10.3 ± 0.4 and 15.5 ± 1.1 mg C_{mic} g^{-1} d.m. soil in the homogenised plots and in the surrounding soil, respectively (mean ± S.E.).

3.3. Plant growth and nutrient dynamics

Ant density treatment did not affect the growth, survival, or degree of herbivore damage of the tree seedlings. Spruce seedlings were not visibly damaged by herbivores (survival 98%) and grew steadily from a mean height of 51 cm to 63 cm, whereas pine stems were heavily damaged by herbivores, resulting in only a 50% survival of the seedlings. Besides being moderately damaged by insect herbivores, the birch seedlings suffered also from grazing by hares during autumn 1994, their survival being 71% at the end of the experiment. As the damage caused by hares is not likely to be connected to the ant exclusion, we equalised height differences of the birch seedlings by cutting all seedlings to an equal height of 35 cm in spring 1995.

Concentrations of NH_4^+-N and NO_3^--N in the soil of the homogenised plots decreased during the experiment from 12.8 and 2.3 to 1.8 and 0.9 µg N g^{-1} d.m., respectively. Ant exclusion did not affect mineral N concentrations in the homogenised plots or in the plot surroundings (mean 0.8 µg g^{-1} d.m.), and no differences were found in spruce total N, S, or C contents (mean ± S.E. 288 ± 15, 17 ± 1 mg $plot^{-1}$, and 15 ± 1 g $plot^{-1}$ for N, S, and C, respectively).

4. Discussion

Despite the successful, over 90% reduction of wood ant density, the consequences of this decline to the invertebrate community were surprisingly weak: apart from the positive response of predatory invertebrates, and negative response of the earthworms to the removal of ant colonies in the homogenised plots, we found no effects indicating direct or indirect ant-induced effects either on the forest floor invertebrates, or on the field layer and low canopy vegetation. This observation is not consistent with the relatively common view advocating wood ants to be a keystone taxon in the forest floor and vegetation (e.g. Cherix & Bourne 1980, Laine & Niemelä 1980, Fowler & Macgarvin 1985, Hölldobler & Wilson 1990, Karhu & Neuvonen 1998).

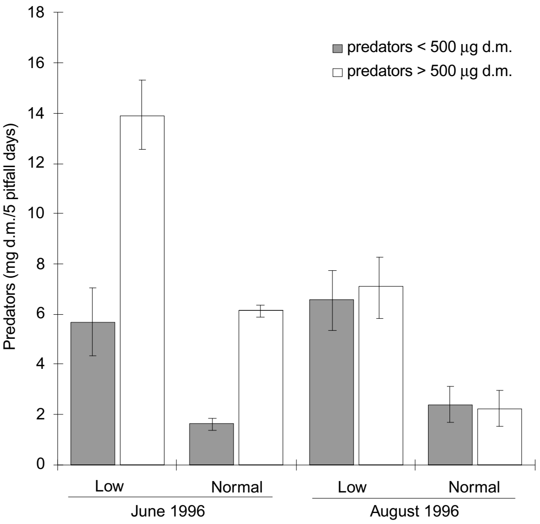

Fig. 1. Biomass of small and large arthropod predators (body mass < 0.5 mg d.m. and > 0.5 mg, respectively) in pitfalls placed in the homogenised plots in June and August 1996. Low = reduced ant density, normal = normal ant density.

One plausible explanation for the observed rarity of ant-induced effects in the forest floor is that wood ants are predominantly adapted to forage on tree trunks and in the foliage (Skinner 1980, Rosengren & Sundström 1991, Whittaker 1991) rather than in the litter layer. However, this explanation does not take into account the negative influence of ants on other predators in the forest floor (Cherix & Bourne 1980, Niemelä *et al.* 1992, Laakso 1999, this study), and fails to explain the unresponsiveness of the fauna in the field layer and low canopy vegetation to changes in ant density. The observed increase in the activity of arthropod predators in plots with low wood ant density implies that the reduction of wood ant density was followed by a compensatory change in the composition of the invertebrate predator guild. The interference of other insect predators (Halaj *et al.* 1997) and competition for food by wood ants (Aho 1997) can force predators to forage in habitats with lower wood ant density and hence compensate changes in wood ant density. Further, ant-induced compensatory changes have also been documented to exist in the foliage herbivore community: the presence of herbivore species with strong defences against ants, or species having mutualistic relationship with wood ants can partially buffer changes in the total prey biomass (Fowler & Macgarvin 1985, Rosengren & Sundström 1991, Whittaker 1991). Thus, we suggest that the high number of alternative prey and predator species, antipredatory adaptations, and complex spatial structure of the soil offering refuge strongly decrease the potential of individual predator species to influence the invertebrate community in the boreal forest floor and vegetation. The generally weak responses of the invertebrate community to ant removal, together with the apparent compensatory changes in the predator community give support to the view that in complex and species rich food webs the propagation of top-down effects is weak (Polis & Strong 1996).

The observed negative response of earthworms to ant removal demonstrates that earthworms are an exception among the generally unresponsive fauna. In our previous studies we have shown that earthworm biomass (Laakso & Setälä 1998) and reproduction (Laakso 1999) can be positively associated with ants, and that earthworms are rarely predated by wood ants (Laakso & Setälä 1997). The increase in predator biomass and decrease in earthworm biomass at low ant density suggests that these predators negatively influenced earthworms. This appears to be especially true in the homogenised plots with a thin and loosely structured organic layer that appears to be more accessible to predators. We have previously hypothesised that the high density of earthworms in ant nest mounds is caused by a combination of favourable physio-chemical conditions, high amount of food resources, and the low density of predators other than ants (Laakso & Setälä 1997, 1998). In this experiment neither soil physio-chemical conditions nor amount of food (i.e. microbial biomass) differed between the homogenised plots with low and high ant density. Thus, it seems that ant-induced declines in the abundance of predators can alone cause the increase in earthworm density. Although the role of predators in regulating earthworm biomasses is generally considered small (Judas 1989, Edwards & Bohlen 1996), epigeic earthworm species, such as *D. octaedra* in this study, are considered to be most vulnerable to predators (Edwards & Bohlen 1996). Thus, it appears that the negative interaction between wood ants and other invertebrate predators significantly modifies the strength of top-down control on earthworm biomasses in boreal forest soil.

As earthworms are known to significantly affect nutrient mineralisation and soil physical properties (e.g. Haimi & Einbork 1992, Edwards & Bohlen 1996), the indirect relationship between wood ants and earthworms has also a potential to be functionally important. However, despite the positive effect of ants on earthworms, we did not observe changes in nutrient cycling and growth of the tree seedlings during the three-year experiment. This is not surprising in the light that the earthworm biomass in the study area was on average less than one third of the biomass of microbi-detritivorous fauna. Moreover, there is evidence that many microbivorous and detritivorous species are functionally redundant, suggesting that only large changes in the structure of the food web can reflect to system functioning (Andrén *et al.* 1995, Laakso & Setälä 1999).

The nest building activity of wood ants have also been proposed to directly promote nutrient cycling in and near the nest mounds (White 1985). Although this effect has been shown to exist in the nest mounds (Pokarzhevskij 1981, Froutz *et al.* 1997, Karhu & Neuvonen 1998), our data on the unchanged levels of mineral N, and plant N uptake suggest that this phenomena does not extend outside the nest mounds.

To conclude, we propose that the structure and functioning of the detrital food web outside the nest mounds can be indifferent to changes in the density of wood ants. Several mechanisms, including spatial separation of wood ants from soil fauna, antipredatory defences, compensatory changes in the predator community, and the insensitivity of system functioning to changes in the structure of detrital community can contribute to this outcome in the boreal forest floor.

ACKNOWLEDGEMENTS: The members of Soil Research Group in Jyväskylä, and enforcements from the GSF institute made the war against ants in the study area victorious. Jussi Päivinen and Esko Hyvärinen identified the arthropods in pitfall and sweep-net samples. Petri Ahlroth, Jari Haimi and Veikko Huhta helped with other arthropods. Mervi Karppanen, Pia Heikkinen, Tuula Hämäläinen, Katja Hänninen, Kati Laitinen, Heli Liukku, Kirsi Ruotsalainen and Titta Räisänen provided help in the practical phases of the work. The study was sponsored by the Academy of Finland and University of Jyväskylä.

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