Forest stand structure, site type and distribution of ant mounds in boreal forests in Finland in the 1950s

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To clarify the association of the occurrence and density of ant mounds (*Formica rufa* group and other mound-building ants) with forest habitat attributes, such as stand structure and successional stage, we reanalyzed the data of the third Finnish National Forest Inventory from 1951–1953. Mound occurrence (presence *vs.* absence) on the sample plots was highest in medium-rich and medium-dense spruce- and birch-dominated forests. In southern Finland, mounds occurred more frequently in older than in younger forest development classes. Mound density (numbers counted on 0.1 ha circular sample plots) was best associated with latitude, with decreasing density towards the north, and averaged 0.25 mounds per 0.1 ha. In addition, density was highest on fine sandy soils. In sum, the habitat attributes related to climate, productivity, light conditions and food resource availability seemed to be key factors determining the distribution of ant mounds. For future surveys, we suggest that additional information on ant species, mound size and colony vitality should be included to explain mound distribution in more detail.

Introduction

Territorial ants are ecologically dominant in many ecosystems around the world. In Eurasian temperate and, especially, boreal forests, several groups of territorial ants, including the mound-building wood ants (*Formica rufa* group) are considered keystone species affecting the ecosystem in several ways. Wood ants are extremely common in many forest habitats and can be found throughout Finland from the southern hemiboreal to subarctic zone (Wuorenrinne 1974, Rosengren *et al.* 1979, Laine & Niemelä 1989). Wood ants defend their large territories against other ant species, especially against other territorial and aggressive species (Mabelis 1984, Savolainen & Vepsäläinen 1988, 1989). They use forest litter and resin to build large above-ground mound nests (e.g. Hölldobler & Wilson 1990, Laakso & Setälä 1998). They also

accumulate nutrients in the mounds (e.g. Lenoir *et al*. 2001), mix soil and alter its structure (e.g. Pokarzhevskij 1981), prey on many invertebrates (e.g. Stradling 1978), tend sap-sucking aphids and, apparently, affect tree growth (e.g. Wellenstein 1980, Rosengren & Sundstöm 1991, cf. Mahdi & Wittaker 1993).

Although the general distribution of wood ant species is fairly well known owing to extensive studies in many Eurasian countries either on a local scale (e.g. Sudd *et al*. 1977, Klimetzek 1981, Laine & Niemelä 1989) or a national scale (e.g. Baroni Urbani & Collingwood 1977, Seifert 1991, Reznikova 2003), the data are rarely based on systematic sampling across all forest site types and successional stages. In Finland, however, a national ant mound inventory was carried out as a part of the third National Forest Inventory (NFI3) in the beginning of the 1950s with the intention to assess the density of the ecologically dominant wood ants of the *Formica rufa* group (Ilvessalo 1951, 1956), which at the time was considered an integral part of pest control of managed forests (*see* the review by Adlung 1966). At that time, myrmecological research was in its infancy in Finland, so data on species identity were unfortunately not collected. The different species of mound-building ants require slightly different types of habitats, so the relationships between mound density and forest stand structure can be confounded by species turnover across habitat types and successional stages (Punttila 1996). This may be of importance when assessing the ecological importance of mound-building ants. Similarly, information on mound vitality was not recorded and thus, the data may include also abandoned mounds. For instance, wood ants may survive for a few years after clear-cutting but often the colonies are abandoned (Rosengren *et al*. 1979) resulting in increased proportion of abandoned mounds in seedling stands (*see* table 2 in Punttila 1996). Neither mound size was recorded although it could have helped in assessing the timing of colony establishment and the ecological impact of ants if we rely on the generally accepted view that larger mounds have larger colonies (e.g. Seifert 1991). Finally, a 0.1 ha plot size is rather small to study the ant mound density and leads to a large proportion of sample plots without ant

mounds. However, the large number of sample plots mitigates to some extent the shortcomings. These drawbacks limit the strength of the conclusions that can be drawn from the data, but still allow a general view of the situation over 50 years ago.

Forest management and its intensity and thus, forest structure, have changed considerably since the 1950s. At that time forests were still logged manually and the timber was transported primarily by horses and by floating. Although selective logging (trees larger than a certain diameter logged) was banned in the 1940s (Mikola 1984), selectively logged stands were still frequently encountered in the NFI3. Selective logging was replaced by thinning to promote the growth of the best trees in the stands, and the forests were regenerated by planting or naturally by retaining seed trees after clear-cutting (Valtanen 1996). In the 1950s more than half of the forests in Finland were dominated by Scots pine (*Pinus sylvestris* L.), almost a third by Norway spruce (*Picea abies* (L.) Karst.), and the rest by deciduous trees, mostly birch species (*Betula* spp.) (Ilvessalo 1956). At that time, the proportion of 41- to 60-year-old forests was greatest in southern Finland, while over 140-year-old forests were most abundant in the north (Peltola 2004). Intensive ditching to accelerate forest growth peaked in the late 1960s, but has ceased recently (Peltola 2004). In the early 1950s, less than ten percent of the mires of Finland were ditched (Ilvessalo 1956), and by the early 2000s, over half (ca. 48 800 km^2 or 18.6% of the forestry land) of the mires were ditched (Peltola 2004).

In mature Finnish forests, most ant mounds represent species of the *Formica rufa* group, *F. rufa* L., *F. polyctena* Först., *F. aquilonia* Yarr., *F. lugubris* Zett. and possibly *F. paralugubris*, while *F. pratensis* Retz. and other mound-building species such as *F. uralensis* Ruzs. and species of the *F. exsecta* group are abundant in open forests, meadows or mires (Collingwood 1979, Punttila 1994, 1996, Seifert 1996, Sundström *et al*. 2005). In Finland, *F. rufa* and *F. lugubris* are mainly monogyne (one queen) and monodomous (single-mound colony), whereas *F. polyctena* and *F. aquilonia* colonies are polygyne and polydomous (multi-queen, multi-mound colonies) (Rosengren & Pamilo 1983). Monogyne

species are often considered to be better long-distance dispersers than polygyne species (*see* Sundström *et al.* 2005), but a recent genetic study has questioned this view in *F. exsecta* (Sundström *et al.* 2003). Monogyne wood ants tend to be more common in young forests and in small, isolated fragments of mature forest, whereas polygyne and polydomous wood ants are dominant in mature, continuous forests (Savolainen & Vepsäläinen 1988, 1989, Punttila 1996). Among the highly polygyne species, the most common one in Finland, *F. aquilonia*, is found throughout the country, while *F. polyctena* appears to be more restricted to southern Finland (Wuorenrinne 1974, Baroni Urbani & Collingwood 1977, Rosengren *et al.* 1979). Among the monogyne or weakly polygyne species, *F. lugubris* is found throughout Finland from the archipelago of the Gulf of Finland to subarctic forests of northern Finland (Rosengren *et al.* 1979, Laine & Niemelä 1989) and is very common in young forests in southern Finland (Punttila 1996), whereas *F. rufa* occurs mainly in the hemi- and south-boreal forests (Wuorenrinne 1974).

Colonization of an area by ants depends on the habitat requirements and the dispersal and colonization capacities of the species as well as potential species interactions (Vepsäläinen & Pisarski 1982). The composition of ant communities changes during forest succession (Punttila *et al.* 1991, 1994, Punttila 1996). Pioneering ant species capable of independent colony founding are followed by species employing temporary social parasitism during colony foundation (e.g. monogyne wood ant species) and later on, because of the intensified competition among the established colonies, only spreading through colony budding may remain a competitive colonization strategy (e.g. as in polygyne wood ant species) (Punttila *et al.* 1991, 1994, 1996, Seppä *et al.* 1995, Punttila 1996, *see* also Oinonen 1956). The species composition also appears to correlate with light conditions in the forest such that monogyne wood ants often dominate until canopy closure, whereas especially larger mature stands are often dominated by highly polygyne wood ants (Punttila 1996). Presumably, a well-populated ant colony in a large mound can maintain independent thermoregu-

lation and thrive in shady habitats more efficiently than a small one (Rosengren *et al.* 1987, Punttila 1996, Sorvari & Hakkarainen 2005). The main resource for the ants of the *F. rufa* group is honeydew excreted by aphids (Rosengren & Sundström 1991). Aphids are present in most forest habitats, although the taxa mostly used by the ants (*Cinara* spp., cf. Rosengren & Sundström 1991) can only survive in the presence of ants. However, once a habitat has been colonized by ants these aphids are also likely to be present. Ants can even manipulate the aphid density in their feeding territory (Vepsäläinen & Savolainen 1994), and use the surplus of tended aphids as a source of protein (Rosengren & Sundström 1991). Nevertheless, a richer habitat may be assumed to maintain a denser population of aphids and more diverse other food resources and thus a higher ant mound density than a poorer one.

Earlier, Wuorenrinne (1974) and Rosengren *et al.* (1979) analyzed subsets of the NFI3 data with respect to the number of ant mounds and assumed that the data encompassed mainly the *Formica rufa* group. Wuorenrinne (1974) analyzed the occurrence (presence *vs.* absence) of ant mounds, and Rosengren *et al.* (1979) also mound density in south-western and central Finland. The authors found the highest occurrences and densities of ant mounds in southern Finland, and in medium-rich, medium-dense, mixed forests, and concluded that factors related to vegetation, food resources and climate were the main determinants of mound distribution. In the present paper, we analyze the occurrence and density of ant mounds on mineral soils in the entire mainland Finland, except the northernmost parts, and include a larger range of habitat attributes, such as soil type and silvicultural development class in the analysis. These data serve in revealing the general large-scale variation of mound occurrence and density along the major ecological gradients in boreal forests and can to some extent be interpreted with the aid of the present ecological knowledge of mound-building ants. The aim of this study is to explain how the occurrence and density of ant mounds are associated with forest site type, soil type, forest stand structure and forest succession in different parts of Finland.
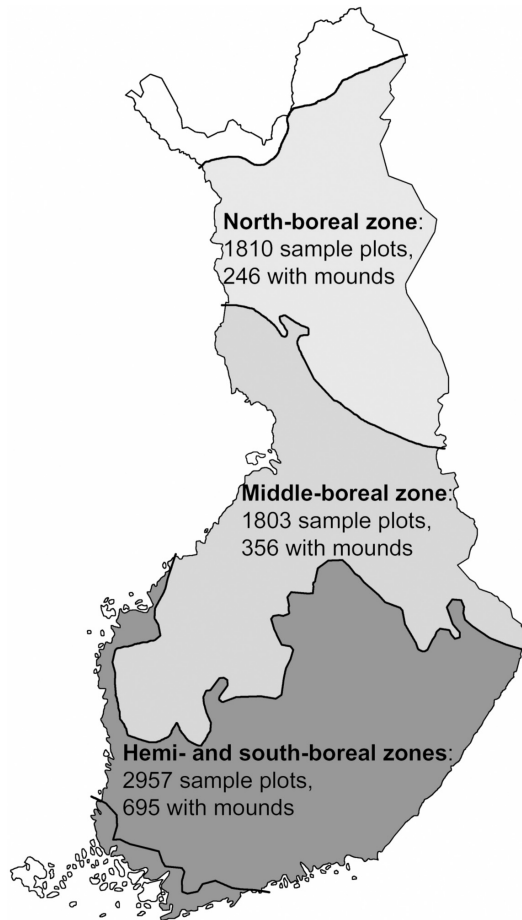
Fig. 1. Number of sample plots in the vegetation zones. White areas were excluded from the analyses (simplified from Kalela (1960) and Ahti *et al.* (1968)).

Material and methods

The third National Forest Inventory

The third National Forest Inventory (NFI3) was carried out during 1951–1953 as a line survey (Ilvessalo 1951, 1956). The distance between the southwest–northeast lines was 13 km in southern and central Finland and 16 km in northern Finland. Detailed measurements of a range of variables describing forest characteristics and the number of ant mounds were made on 0.1 ha circular sample plots situated at one-kilometre intervals along the lines. A total of 6570 sample plots on mineral soils in (a) the hemi- and south-boreal, (b) middle-boreal and (c) north-boreal

zones (Ahti *et al.* 1968) were included in the study (Fig. 1). The hemi- and south-boreal zones were combined because the narrow hemi-boreal zone contained alone too few sample plots. Similarly, the northernmost parts of Finland were excluded from the study because an extensive area would have been represented by a very small number of sample plots.

The sample plots were categorized into five site-type classes: (1) groves (OMaT, *Oxalis-Maianthemum* type and related site types) and rich sites (OMT, *Oxalis–Myrtillus* type and related site types), (2) medium-rich sites (MT, *Myrtillus* type and related site types), (3) medium-poor sites (VT, *Vaccinium* type and related site types), (4) poor sites (CT, *Calluna* type and related site types), and (5) very poor sites (ClT, *Cladonia* type and related site types) and rocky sites according to the Finnish site type classification (Cajander 1926, 1949). In the NFI3, the dominant tree species on a sample plot was the species with the highest stand volume (Ilvessalo 1951). Four dominant tree species were distinguished: (1) Scots pine (*Pinus sylvestris* L.), (2) Norway spruce (*Picea abies* (L.) Karst.), (3) birch (*Betula pendula* Roth., *B. pubescens* Ehrh.), and (4) other deciduous species (mostly aspen (*Populus tremula* L.) and alder (*Alnus* Mill. spp.)).

The density of the dominant tree storey was estimated on a scale of 1–11 according to how the trees (taking the tree species and age into account) filled their growing area. A silviculturally normal density was selected as the basic density, 10. Over-dense forests were given a density value of 11. Forest density was combined into four classes: 1 = 1–3, 2 = 4–6, 3 = 7–8, and 4 = 9–11. The age of the dominant tree storey was defined by counting annual rings from increment core samples or stumps of recently logged trees, or by counting the number of annual growth sections up the stem. Age was categorized into six classes: 1 = 0–40, 2 = 41–60, 3 = 61–80, 4 = 81–100, 5 = 101–130, and 6 = more than 131 years.

Six development classes were determined for viable forest stands (*n* = 4014; selectively logged stands and non-viable stands, *viz.* stands damaged by reckless cutting, stands with unsuitable tree species, over-aged stands and stands to be regenerated for other reasons, e.g. for poor

health, not included): 1 = open regeneration areas, 2 = seedling stands, 3 = young thinning stands, 4 = advanced thinning stands, 5 = mature stands, and 6 = shelterwood and seed-tree stands. Open regeneration areas were the youngest and mature stands the oldest areas in the forest succession gradient. Seed-tree stands had sparse cover of large trees that were left to regenerate the area naturally, and from the point of view of ants these should correspond to open regeneration areas. Shelterwood stands had sparse cover of large trees that were left usually to cover frost prone seedlings. For ants these stands probably better correspond to seedling stands, but unfortunately, shelterwood and seed-tree stands could not be separated.

Particle size distribution was determined on soil samples taken from ca. 30 cm deep pits dug in the centre of the plots. The soil was classified according to the dominant particle size into the following groups: 1 = sorted gravel (grain size 2–20 mm) and gravel till, 2 = sorted coarse sand (0.2–2 mm) and coarse sand till, 3 = sorted fine sand (0.02–0.2 mm) and fine sand till, 4 = sorted silt and clay (0.002–0.02 mm) and their till forms, and 5 = rocky soils. In addition, stem number and basal area by tree species were determined on each sample plot.

Statistical analyses

We used log-likelihood ratio test to analyze the relationships between mound occurrence, expressed as the presence or absence of mounds in a sample plot, and individual habitat attributes in the three vegetation zones: (a) hemi- and south-boreal, (b) middle-boreal, and (c) north-boreal zones. We tested whether the numbers of sample plots without and with at least one ant mound were distributed in similar proportions across stands of different site type, dominant tree species, forest density, forest age and development classes. The differences in the numbers of sample plots with and without ant mounds in the contingency tables were interpreted from standardized residuals of the log-likelihood ratio tests, when statistically significant differences were found. The significance values were adjusted with the sequential Bonferroni technique (Rice

1989). The log-likelihood ratio tests were calculated with SPSS 12.0.1.

To investigate the relationships between habitat attributes and the density of ant mounds per 0.1 ha, we processed the data for the combined three vegetation zones with Poisson regression analysis (Table 1). In this analysis, the response variable was transformed into the natural logarithm in order to link it to the linear function of the explanatory variables. Due to missing cases, forest density and development class were not included in the analysis. Each class (except the class with the highest number of cases, the reference class) of the classified variables was represented by dummy variables, and so we could exclude redundant classes from the analysis. Independent dummy variables of site type and dominant tree species and their interaction terms with stand age were included, and dummy variables were also formed for soil type. Explanatory variables other than dummy variables were standardized to have a mean of 0 and a variance of 1. We used backward selection to select explanatory variables, and the criterion of statistical significance for variables to remain in the model was selected to be quite strict ($p < 0.005$) because the large sample size decreases significance values (McBride *et al.* 1993). The sample plot with the largest number of ant mounds (15 mounds per 0.1 ha) was excluded from the Poisson regression analysis as an outlier, because

Table 1. List of variables included in the Poisson regression analysis.

Dependent variable
    Number of ant mounds per 0.1 ha

Independent variables
    Latitude
    Forest age (years)
    Basal area of pines ($m^2 ha^{-1}$)
    Basal area of spruces ($m^2 ha^{-1}$)
    Basal area of birches ($m^2 ha^{-1}$)
    Basal area of other deciduous trees ($m^2 ha^{-1}$)
    Stem number of pines (ha^{-1})
    Stem number of spruces (ha^{-1})
    Stem number of birches (ha^{-1})
    Stem number of other deciduous trees (ha^{-1})
    Forest site type class (1–5)
    Dominant tree species (1–4)
    Soil type according to dominant particle size (1–5)
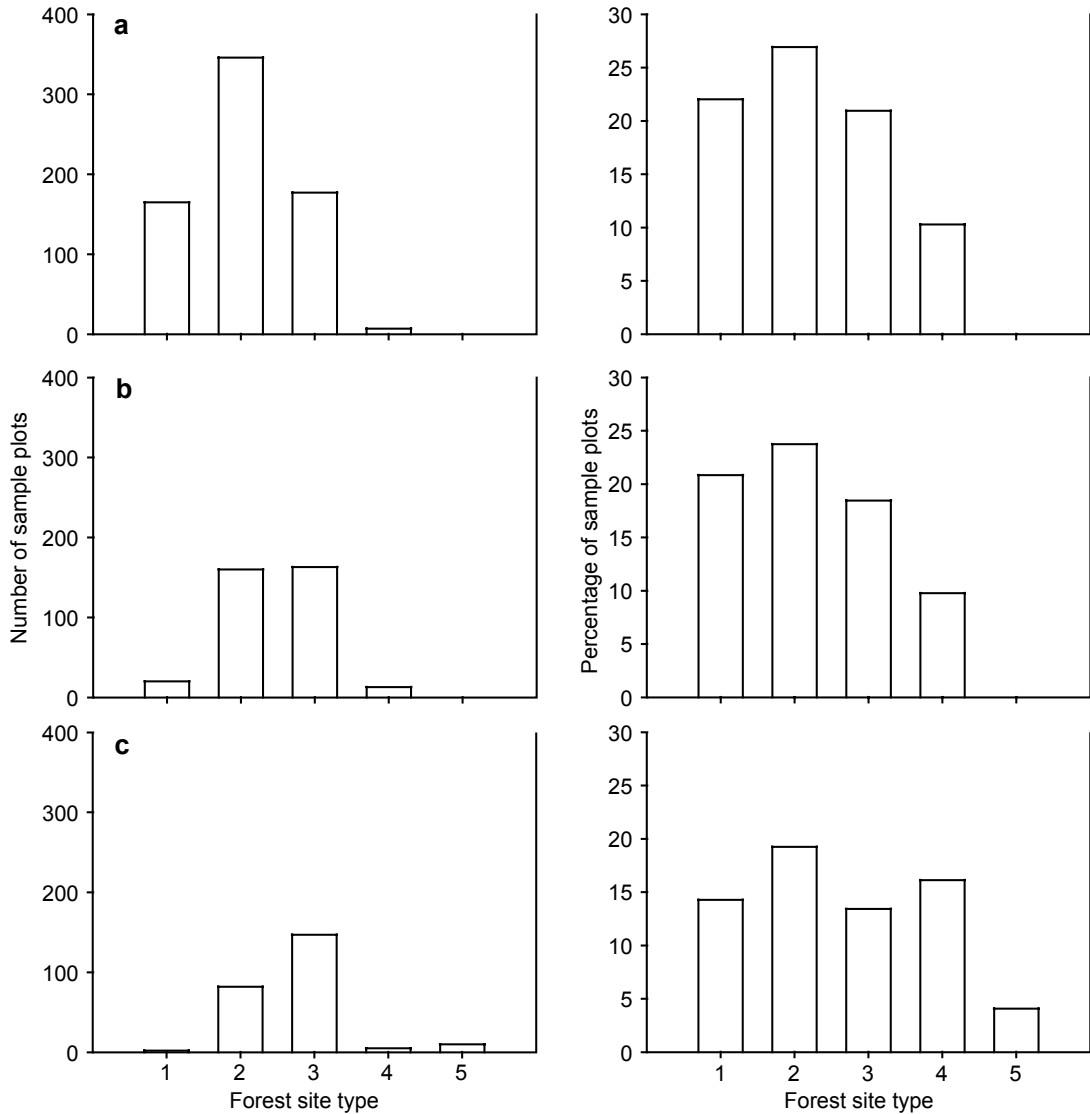
Fig. 2. Total number (left) and percentage (right; percentage of all plots) of sample plots with at least one ant mound in classes of forest site type (1 = groves and rich sites, 2 = medium-rich sites, 3 = medium-poor sites, 4 = poor sites, 5 = very poor and rocky sites) in (**a**) hemi- and south-, (**b**) middle-, and (**c**) north-boreal zones. In zones **a** and **b** there were no sample plots with ant mounds on very poor and rocky sites. The letters **a**, **b** and **c** also refer to the respective panels in the right-hand column.

it received too large a weight and gave unfair importance to variables that were otherwise not connected to high mound density. The Poisson regression model was fitted by Newton-Raphson algorithm with Egret 2.0.31.

Owing to multicollinearity among the variables, we applied principal components analysis to combine several variables, but as this did not reduce the number of variables we used the orig-

inal ones in the Poisson regression analysis. To assess the relative importance of each selected explanatory variable, we applied hierarchical partitioning (Chevan & Sutherland 1991, Mac Nally 1996). In this procedure, all possible combinations of explanatory variables are formed to construct models which are considered as a hierarchy (0, 1, 2, 3, etc. explanatory variables). The improvement in model fit following the

inclusion of a particular explanatory variable is calculated and the outcome averaged across all the model hierarchies in which this particular variable occurs. The same logic is largely used to divide the joint contribution of a particular variable. Hierarchical partitioning produces the average independent and joint contribution of each explanatory variable to the goodness-of-fit of the full model, here log-likelihood. We run hierarchical partitioning with the hier.part package version 1.0 (Walsh & Mac Nally 2004) as a part of R 2.0.1 statistical software (R: A language and environment for statistical computing, 2004).

Results

Most of the sample plots (80.3%) housed no ant mounds, and 3.6% of the plots had more than one ant mound. Among the classes of forest site type, the proportion of sample plots with ant mounds (mound plots) was higher than expected by chance in medium-rich forests in all vegetation zones (Fig. 2 and Table 2). Poor stands in the north-boreal zone had slightly more mound plots than expected, whereas in

the other zones, poor stands had fewer mound plots than expected by chance. In the hemi- and south-boreal zones, birch- and spruce-dominated stands had more mound plots than expected, and in the north-boreal zone, spruce-dominated forests had more mound plots than expected by chance (Fig. 3 and Table 2). Medium-dense forests with a density class of 4–6 had more mound plots than expected by chance in the hemi- and south-boreal zones (Fig. 4 and Table 2), but the occurrence of ant mounds was not associated significantly with the stand age (Fig. 5 and Table 2). In the hemi- and south-boreal zones, shelterwood and seed-tree stands and especially mature stands had more, and open regeneration areas, and seedling stands fewer mound plots than expected by chance (Table 2 and Fig. 6). In the north-boreal zone, young thinning stands had more, mature stands slightly more, and seedling stands and shelterwood and seed-tree stands fewer mound plots than expected by chance (Table 2 and Fig. 6).

The mean mound density across the entire country was 0.25 mounds 0.1 ha^{-1}, and 0.31, 0.24 and 0.15 mounds 0.1 ha^{-1} in the hemi- and south-boreal, middle-boreal and north-boreal

Table 2. Log-likelihood ratio test statistics in the vegetation zones testing the null-hypothesis that states the numbers of sample plots with at least one ant mound and without ant mounds to be distributed similarly among classes of forest site type, stands of different dominant tree species and forest density, forest age and development classes. Sequential Bonferroni adjusted *p* values are presented in Adj. *p* rows, where boldface shows significance and NS non-significance, when table-wide $\alpha = 0.05$.

Independent variable	df		Hemi- and south-boreal	Middle-boreal	North-boreal
Forest site type	4	G^2	25.419	24.416	35.690
		p	< 0.0001	< 0.0001	< 0.0001
		Adj. *p*	**0.0036**	**0.0038**	**0.0033**
Dominant tree species	3*	G^2	17.608	6.932	16.790
		p	0.0005	0.0741	0.0002
		Adj. *p*	**0.0050**	NS	**0.0045**
Forest density	3	G^2	19.523	3.348	7.974
		p	0.0002	0.3410	0.0466
		Adj. *p*	**0.0042**	NS	NS
Age class	5	G^2	8.584	6.419	3.842
		p	0.1268	0.2675	0.5723
		Adj. *p*	NS	NS	NS
Development class	5	G^2	16.529	5.520	16.506
		p	0.0055	0.3557	0.0055
		Adj. *p*	**0.0056**	NS	**0.0063**

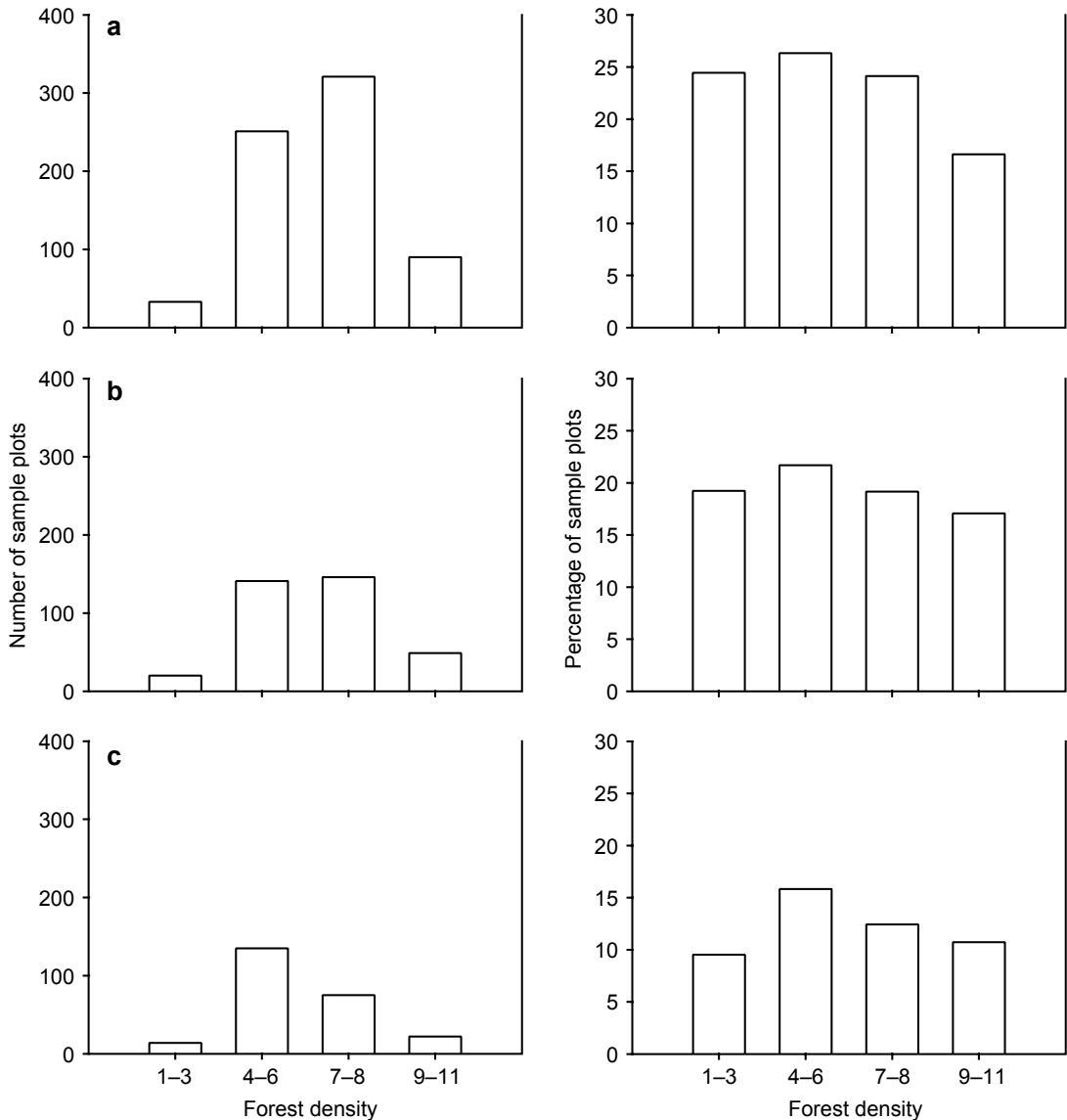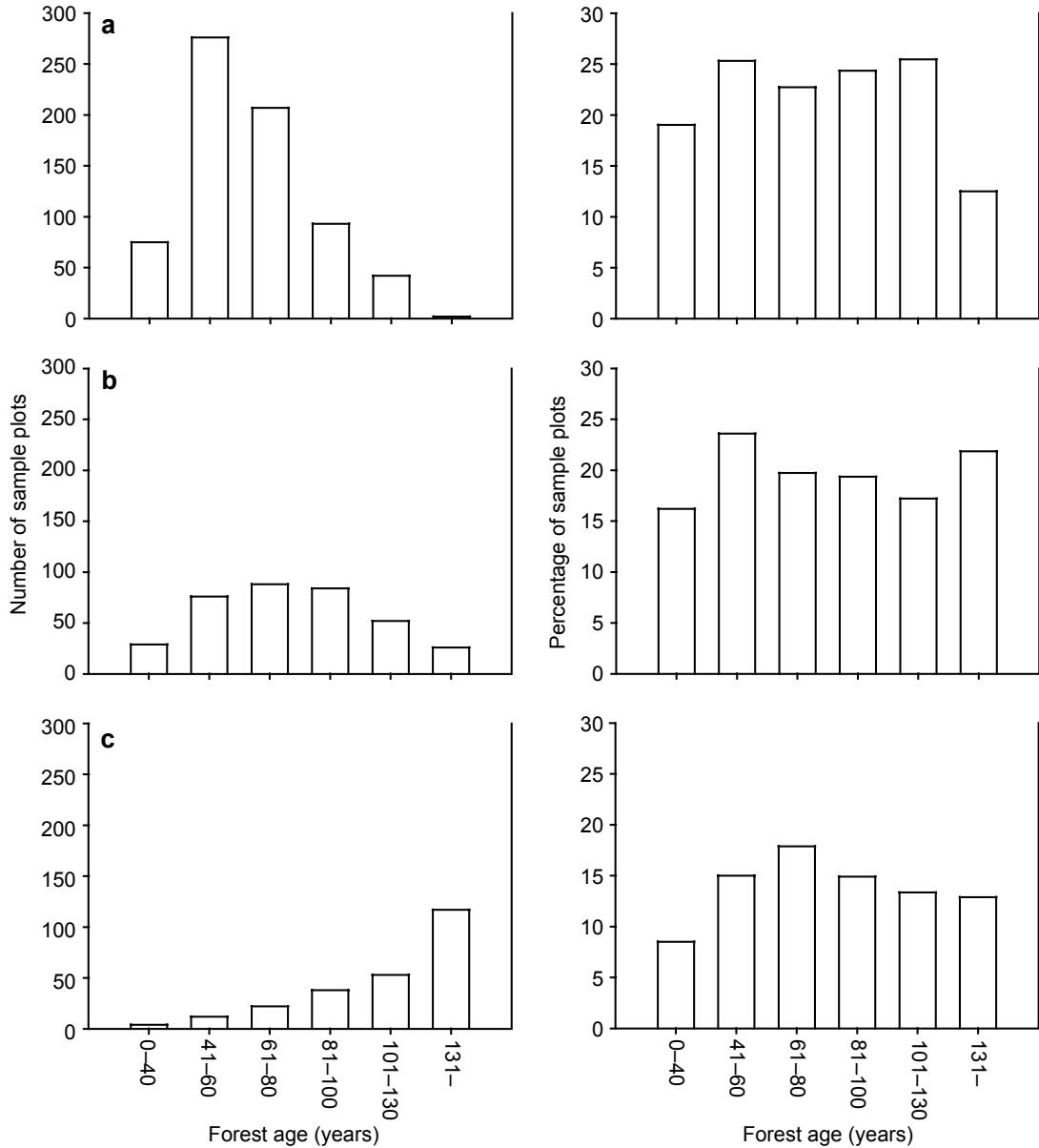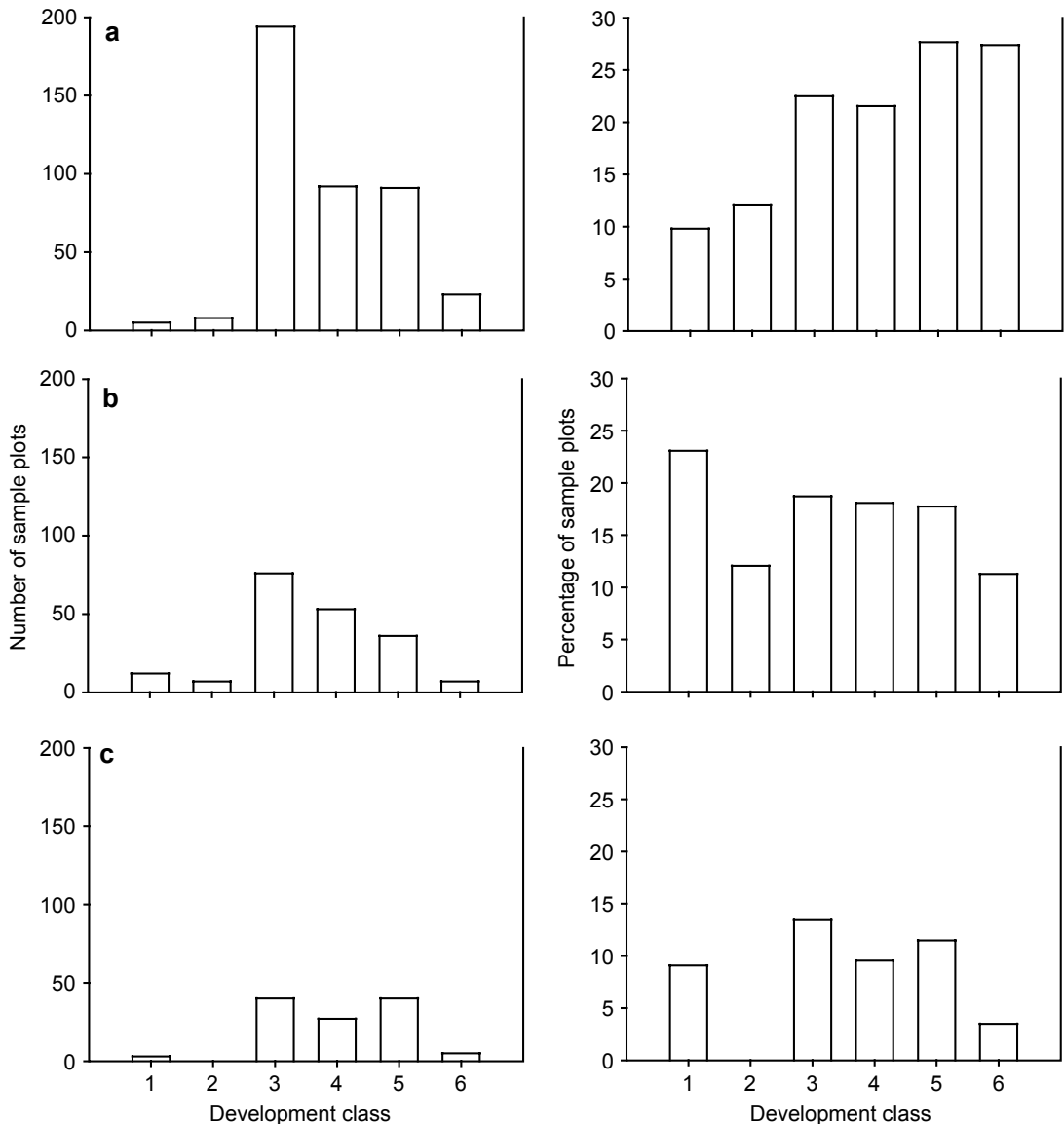*In the north-boreal zone the degree of freedom was 2.
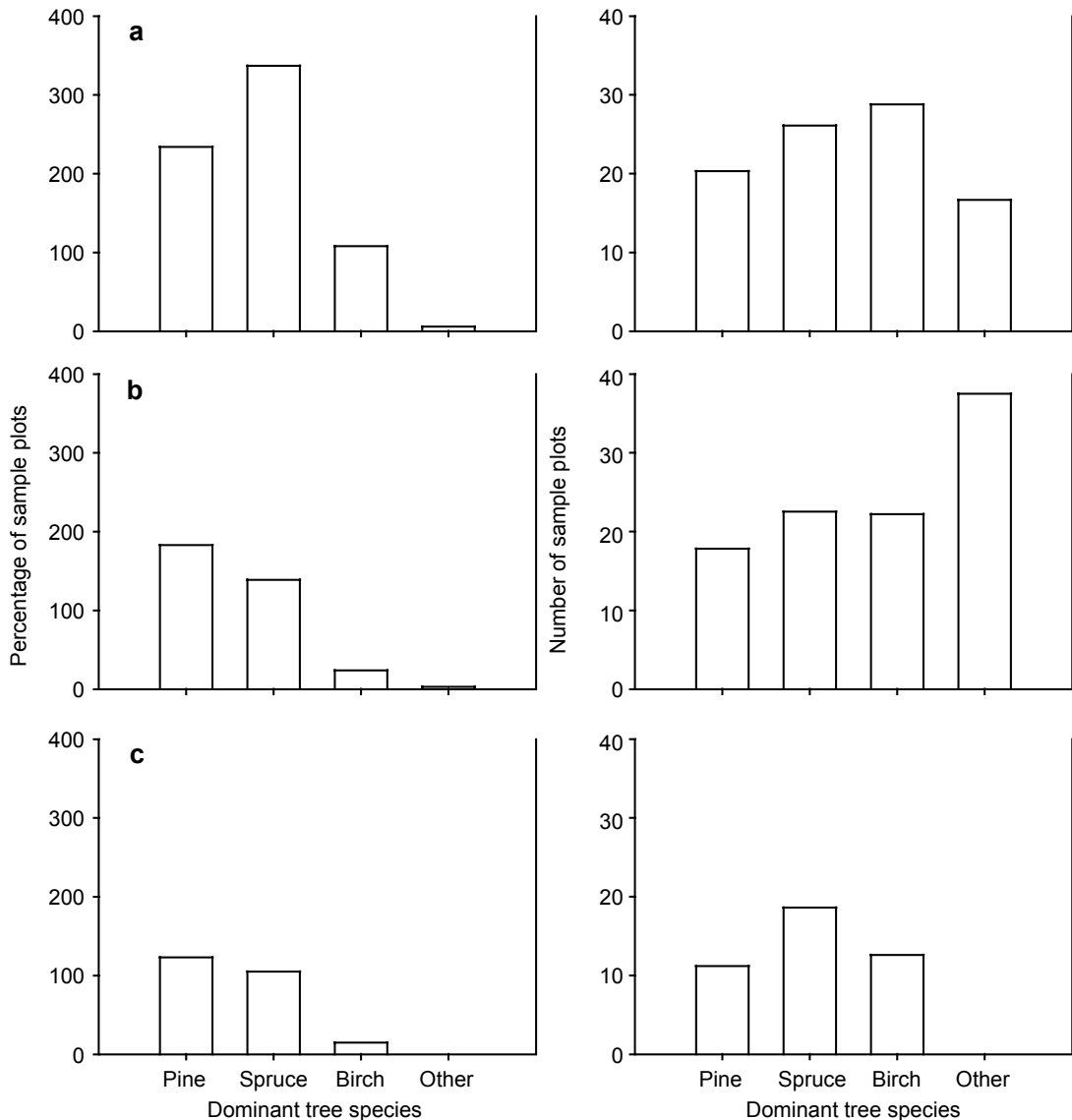
Fig. 3. Total number (left) and percentage (right; percentage of all plots) of sample plots with at least one ant mound in classes with different dominant tree species in (**a**) hemi- and south-, (**b**) middle-, and (**c**) north-boreal zones. In zone **c** there were no observations in the "Other" category. The letters **a**, **b** and **c** also refer to the respective panels in the right-hand column.

zones, respectively. The mound density in different classes of the explored habitat attributes fluctuated similarly to the variation in mound occurrence (Figs. 2–6), except that in the north-boreal zone the mound density was highest on poor sites and birch-dominated stands, and in the hemi- and south boreal zones in the class of the lowest forest density.

The density of ant mounds decreased with

latitude (Table 3). Stands with a high basal area of Scots pine had low mound densities. Mound density was higher on fine sandy soils than on coarse sandy soils (the reference class). Mound density was higher on medium-rich sites and lower on very poor and rocky sites than on medium-poor sites (the reference class). Most of the explained variation in the Poisson regression model was attributable to independent contribu-

Fig. 4. Total number (left) and percentage (right; percentage of all plots) of sample plots with at least one ant mound in classes of forest density (class 1 refers to an open area and 11 to an over-dense forest) in (**a**) hemi- and south-, (**b**) middle-, and (**c**) north-boreal zones. The letters **a**, **b** and **c** also refer to the respective panels in the right-hand column.

tions of the variables, and of the explanatory variables, latitude clearly contributed the most to mound density (Fig. 7). The next largest independent contributions (in descending order) were attributable to very poor sites and rocks, basal area of pines, medium-rich sites and fine sand as soil type. Mound density was not affected significantly by the interaction terms of forest site type and dominant tree species with stand age.

Discussion

The present data allow general conclusions about the occurrence and density of ant mounds with respect to forest successional, edaphic and biogeographical attributes in Finland. We found that mound occurrence on the sample plots was highest in southern Finland and in medium-rich and medium-dense spruce- and birch-dominated for-

Fig. 5. Total number (left) and percentage (right; percentage of all plots) of sample plots with at least one ant mound in forest age classes (years) in (**a**) hemi- and south-, (**b**) middle-, and (**c**) north-boreal zones. The letters **a**, **b** and **c** also refer to the respective panels in the right-hand column.

ests, and higher in older than in younger forest development classes. This highlights the importance of adequate illumination and food resources for colony foundation and survival as mound density was highest in medium-dense forests with medium stem numbers and basal areas and lowest in the most open stages following cutting and in the densest forests. Thus, a forest with a density

lower than that targeted by forestry is suitable for ants. The results were consistent with those of previous studies using subsets of the present data (Wuorenrinne 1974, Rosengren *et al.* 1979).

Occurrence and density of ant mounds were highest on medium-rich sites and lowest on very poor and rocky sites. Rich sites most likely offer more diverse food resources for wood ants, pos-

Fig. 6. Total number (left) and percentage (right; percentage of all plots) of sample plots with at least one ant mound in forest development classes (1 = open regeneration areas, 2 = seedling stands, 3 = young thinning stands, 4 = advanced thinning stands, 5 = mature stands, 6 = shelterwood and seed-tree stands) in (**a**) hemi- and south-, (**b**) middle-, and (**c**) north-boreal zones. The letters **a**, **b** and **c** also refer to the respective panels in the right-hand column.

sibly including also a greater diversity of aphid species, and therefore may maintain a higher mound density than poorer sites. However, the richest sites may also have dense vegetation and thus be too shady for ants (Rosengren *et al.* 1979). Furthermore, mound density was highest on fine sandy soils. Fine sandy soils are usually considered to be favourable for plants due to the good aeration and water holding capacities of the soil (Westman 1991). In addition, site richness depends on soil type, and ant mounds were concentrated on the richer sites. Further, fine sandy soils can have more favourable temperature and overwintering conditions than e.g. rocky soils where ants may not be able to overwinter below the frost layer.

Fig. 7. The independent and joint contributions of the explanatory variables to the number of ant mounds 0.1 ha^{-1} (percentage of the total explained variance) in the Poisson regression model (Table 3) estimated with hierarchical partitioning.

mous ones because of the exchange of resources among colony mounds (Rosengren & Pamilo 1983, Punttila 1996). Thus, different species of mound-building ants prevail in different habitats and on the same sites during different stages of forest succession (Punttila 1996). Unfortunately we cannot draw conclusions regarding species composition and species turnover, or about the role of interspecific interactions as the species were not identified during the survey. With these general data, some areal and microclimatic associations, like aggregation of ant mounds on slopes with a southern exposure (Klimetzek 1973, Laine & Niemelä 1989, Maggini *et al.* 2002) and in edge habitats (Klimetzek 1973, Punttila 1996) or the association of mound distribution with stand size cannot be revealed either.

Our analysis suggests that ant mound density decreases towards the north. This may be due to lower fertility and productivity (Tamminen 2000), colder climate and shorter growth season, higher altitude, increased proportion of pine-dominated stands and other changes in forest stand structure (e.g. age class distribution) and also to the turnover of ant species towards the north. Nevertheless, the density of wood ant mounds even in northern Finland was very high

compared e.g. with those reported from central European lowlands (e.g. Klimetzek 1981, Travan 1990). According to recent Swedish National Forest Inventory, ant mound density (active mounds wider than three and higher than two decimetres were counted) was about 2.2 ha^{-1} on mineral soils in nearby Sweden (G. Kempe pers. comm.), a density of the same magnitude as reported here for Finland in the 1950s.

We found that only a small part of the variation in ant mound occurrence and density can be explained by any of the variables explored. This is presumably at least partly due to the confounding drawbacks in the data: small plot size and lack of information on ant species, vitality of ant colonies and mound sizes. Statistical significance appears more easily with large data and does not necessarily imply biological significance (e.g. McBride *et al.* 1993). Nevertheless, in the current data with the large proportion of unexplained variation, even weak associations can be biologically important. Multicollinearity of the variables often complicates the interpretation of results of multiple regression, but we handled this by including only the most influential variables in the Poisson regression model and by hierarchical partitioning (Chevan & Sutherland 1991, Mac Nally 1996) of

the explanatory power of the explanatory variables selected and found that most of the explained variation owed to the independent contributions of the explanatory variables.

Despite some of the drawbacks inherent in these data, our results provide information on the general distribution of ant mounds in Finland over 50 years ago. Since then there have been drastic changes in forest management and structure, and these changes are likely to affect the ant mound density and species composition. For instance, soil preparation might reinforce the devastating effects of clear-cutting through physical damage to the mounds, whereas the current thinning intensity may increase mound numbers because thinning results in better illumination. The smaller size of forest management compartments leads to an increasing proportion of edge habitats which may, to a certain extent, increase the density of ant mounds by providing favourable conditions for colony establishment (Klimetzek 1973, Punttila 1996). Increased proportion of young stands (Peltola 2004) and isolation of mature stands and the reduced stand size of managed forests (e.g. Löfman & Kouki 2003) may have decreased mound density of wood ants by favouring monogyne or weakly polygyne nesting strategies at the expense of obligately polygyne ones (*sensu* Sundström *et al.* 2005), and increased the mound density of other mound-building species of more open habitats (Punttila 1996). On the other hand, ditching to drain mires may have favoured wood ants by creating large areas of new suitable habitat, while species specialized to mires may have declined (Vepsäläinen *et al.* 2000). Any future large-scale distribution or monitoring survey targeting to clarify the above topics should be based on a larger sample unit size, and the data should include species identification and recording of mound size and colony vitality. Aphids should also deserve more emphasis in the distribution studies of aphid-tending ants.

Acknowledgements

References

Adlung, K. G. 1966. A critical evaluation of the European research on use of red wood ants (*Formica rufa* group) for the protection of forest against harmful insects. — *J. Appl. Entomol.* 57: 167–189.

Ahti, T., Hämet-Ahti, L. & Jalas, J. 1968: Vegetation zones and their sections in northwestern Europe. — *Ann. Bot. Fennici* 5: 169–211.

Baroni Urbani, C. & Collingwood, C. A. 1977: The zoogeography of ants. — *Acta Zool. Fennica* 152: 1–34.

Cajander, A. K. 1926: The theory of forest types. — *Acta Forestalia Fennica* 29(3): 1–108.

Cajander, A. K. 1949: Forest types and their significance. — *Acta Forestalia Fennica* 56: 1–71.

Chevan, A. & Sutherland, M. 1991: Hierarchical partitioning. — *The American Statistician* 45: 90–96.

Collingwood, C. A. 1979: The Formicidae (Hymenoptera) of Fennoscandia and Denmark. — *Fauna Entomologica Scandinavica* 8: 1–174.

Hölldobler, B. & Wilson, E. 1990: *The ants.* — Springer-Verlag, Berlin.

Ilvessalo, Y. 1951: III valtakunnan metsien arviointi. Suunnitelma ja maastotyön ohjeet [Third national forest survey of Finland. Plan and instructions for field work]. — *Metsäntutkimuslaitoksen julkaisuja* 39(3): 1–58. [In Finnish with English summary].

Ilvessalo, Y. 1956: Suomen metsät vuosista 1921–24 vuosiin 1951–53. Kolmeen valtakunnan metsien inventointiin perustuva tutkimus [The forests of Finland from 1921–24 to 1951–53. An investigation based on three national forest inventories]. — *Metsäntutkimuslaitoksen julkaisuja* 47(1): 1–227. [In Finnish with English summary].

Kalela, A. 1960: Zones of forest vegetation. — In: Aario, L. (ed.), *Atlas of Finland*, Chapter 10, Flora and vegetation zones, map 17.

Klimetzek, D. 1973: Die Variabilität der Standortansprüche hügelbauender Waldameisen der *Formica rufa*-Gruppe (Hymenoptera: Formicidae) [Habitat requirement variability of mound-building wood ants of the *Formica rufa* group (Hymenoptera: Formicidae)]. — *Mitt. Bad. Landesver. Naturkunde u. Naturschutz* 11(1): 9–25. [In German with English summary].

Klimetzek, D. 1981: Population studies on hill building wood-ants of the *Formica rufa*-Group. — *Oecologia* 48: 418–421.

Laakso, J. & Setälä, H. 1998: Composition and trophic structure of detrital foodweb in ant nest mounds of *Formica aquilonia* and in the surrounding forest soil. — *Oikos* 81: 266–278.

Laine, K. J. & Niemelä, P. 1989: Nests and nest sites of red

wood ants (Hymenoptera, Formicidae) in subarctic Finland. — *Ann. Entomol. Fennici* 55: 81–87.

Lenoir, L., Persson, T. & Bengtsson, J. 2001: Wood ant nests as potential hot spots for carbon and nitrogen mineralization. — *Biol. Fertil. Soils* 34: 235–240.

Löfman, S. & Kouki, J. 2003: Scale and dynamics of a transforming forest landscape. — *Forest Ecology and Management* 175: 247–252.

Mabelis, A. A. 1984: Interference between wood ants and other ant species (Hymenoptera, Formicidae). — *Netherlands Journal of Zoology* 34(1): 1–20.

Mac Nally, R. 1996: Hierarchical partitioning as an interpretative tool in multivariate inference. — *Australian Journal of Ecology* 21: 224–228.

Maggini, R., Guisan, A. & Cherix, D. 2002: A stratified approach for modeling the distribution of a threatened ant species in the Swiss National Park. — *Biodiversity and Conservation* 11: 2117–2141.

Mahdi, T. & Whittaker, J. B. 1993: Do birch trees (*Betula pendula*) grow better if foraged by wood ants? — *Journal of Animal Ecology* 62: 101–116.

McBride, G. B., Loftis, J. C. & Adkins, N. C. 1993: What do significance tests really tell us about the environment — *Environmental Management* 17: 423–432.

Mikola, P. 1984: Harsintametsätalous [Selection system]. — *Silva Fennica* 18: 293–301. [In Finnish with English summary].

Müller, H. 1960: Der Honigtau als Nahrung der hügelbauenden Waldameisen. — *Entomophaga* 5: 55–75.

Oinonen, E. 1956: Kallioiden muurahaisista ja niiden osuudesta kallioiden metsittymiseen Etelä-Suomessa [On the ants of the rocks and their contribution to the afforestation of rocks in southern Finland]. — *Acta Entomologica Fennica* 12: 1–212. [In Finnish with English summary].

Peltola, A. (ed.) 2004: Metsätilastollinen vuosikirja [Finnish Statistical yearbook of forestry]. — *SVT Agriculture, forestry and fishery* 2004(45): 1–416. [In Finnish with English summary].

Pokarzhevskij, A. D. 1981: The distribution and accumulation of nutrients in nests of ant *Formica polyctena* (Hymenoptera, Formicidae). — *Pedobiologia* 21: 117–124.

Punttila, P. 1994: Kekomuurahaiset ja niveljalkaisyhteisöjen rakenne [Wood ants and the community structure of arthropods]. — *Metsäntutkimuslaitoksen tiedonantoja* 482: 47–58. [In Finnish with English summary].

Punttila, P. 1996: Succession, forest fragmentation, and the distribution of wood ants. — *Oikos* 75: 291–298.

Punttila, P., Haila, Y. & Tukia, H. 1996: Ant communities in taiga clearcuts: habitat effects and species interactions. — *Ecography* 19: 16–28.

Punttila, P., Haila, Y., Niemelä, J. & Pajunen, T. 1994: Ant communities in fragments of old-growth taiga and managed surroundings. — *Ann. Zool. Fennici* 31: 131–144.

Punttila, P., Haila, Y., Pajunen, T. & Tukia, H. 1991: Colonisation of clearcut forests by ants in the southern Finnish taiga: a quantitative survey. — *Oikos* 61: 250–262.

Reznikova, Z. 2003: Distribution patterns of ants in different natural zones and landscapes in Kazakhstan and West Siberia along a meridian trend. — *Euroasian Entomological Journal* 2: 235–242.

Rice, W. R. 1989: Analyzing tables of statistical tests. — *Evolution* 43: 223–225.

Rosengren, R. & Pamilo, P. 1978: Effect of winter timber felling on behaviour of foraging wood ants (*Formica rufa* group) in early spring. — *Memorabilia Zoologica* 29: 143–155.

Rosengren, R. & Pamilo, P. 1983: The evolution of polygyny and polydomy in mound-building *Formica* ants. — *Acta Entomologica Fennica* 42: 65–77.

Rosengren, R. & Sundström, L. 1987: The foraging system of a red wood ant colony (*Formica s. str.*). — *Experimentia,* Suppl. 54: 117–137.

Rosengren, R. & Sundström, L. 1991: The interaction between red wood ants, *Cinara* aphids and pines — a ghost of mutualism past? — In: Huxley, C. R. & Cutler, D. F. (eds.), *Ant–plant interactions*: 80–91. Oxford University Press, Oxford.

Rosengren, R., Vepsäläinen, K. & Wuorenrinne, H. 1979: Distribution, nest densities, and ecological significance of wood ants (the *Formica rufa* group) in Finland. — *O.I.L.B. Bull. SROP*. II-3: 181–213.

Rosengren, R., Fortelius, W., Lindström, K. & Luther, A. 1987: Phenology and causation of nest heating and thermoregulation in red wood ants of the *Formica rufa* group studied in coniferous forest habitats in southern Finland. — *Ann. Zool. Fennici* 24: 147–155.

Savolainen, R. & Vepsäläinen, K. 1988: A competition hierarchy among boreal ants: impact on resource partitioning and community structure. — *Oikos* 51: 135–155.

Savolainen, R. & Vepsäläinen, K. 1989: Niche differentation of ant species within territories of the wood ant *Formica polyctena*. — *Oikos* 56: 3–16.

Seifert, B. 1991: The phenotypes of the *Formica rufa* complex in East Germany. — *Abh. Ber. Naturkundemus. Görlitz* 65: 1–27.

Seifert, B. 1996: *Formica paralugubris* nov. spec. — a sympatric sibling species of *Formica lugubris* from the western Alps (Insecta: Hymenoptera: Formicoidea: Formicidae). — *Reichenbachia Staatliches Museum für Tierkunde Dresden* 31: 193–201.

Seppä, P., Sundström, L. & Punttila, P. 1995: Facultative polygyny and habitat succession in boreal ants. — *Biological Journal of the Linnean Society* 56: 533–551.

Sorvari, J. & Hakkarainen, H. 2004: Habitat-related aggressive behaviour between neighbouring colonies of the polydomous wood ant *Formica aquilonia*. — *Animal Behaviour* 67: 151–153.

Sorvari, J. & Hakkarainen, H. 2005: Deforestation reduces nest mound size and decreases the production of sexual offspring in the wood ant *Formica aquilonia*. — *Ann. Zool. Fennici* 42: 259–267.

Stradling, D. J. 1978: Food and feeding habits of ants. — In: Brian, M. V. (ed.), *Production ecology of ants and termites*: 81–106. Cambridge University Press, Cambridge.

Sudd, J. H., Douglas, J. M., Gaynard, T., Murray, D. M. & Stockdale, J. M. 1977: The distribution of wood-ants (*Formica lugubris* Zetterstedt) in a northern English forest. — *Ecological Entomology* 2: 301–313.

Sundström, L., Keller, L. & Chapuisat, M. 2003: Inbreeding and sex-biased gene flow in the ant *Formica exsecta*.

— *Evolution* 57: 1552–1561.

Sundström, L., Seppä, P. & Pamilo, P. 2005: Genetic population structure and dispersal patterns in *Formica* ants — a review. — *Ann. Zool. Fennici* 42: 163–177.

Tamminen, P. 2000: Soil factors. — In: Mälkönen, E. (ed.), *Forest condition in a changing environment* — *The Finnish case*: 72–86. Kluwer Academic Publishers.

Travan, J. 1990: Bestandsaufnahme der Waldameisennester im Staatswald Oberbayerns — Teil I: Flachlandforstämter. — *Waldhygiene* 18: 119–142.

Valtanen, J. 1996: Metsänhoidon muutokset puolen vuosisadan aikana. — *Metsäntutkimuslaitoksen tiedonantoja* 598: 117–127.

Vepsäläinen, K. & Pisarski, B. 1982: Assembly of island ant communities. — *Ann. Zool. Fennici* 19: 327–335.

Vepsäläinen, K. & Savolainen, R. 1994: Ant-aphid interaction and territorial dynamics of wood ants. — *Memorabilia Zoologica* 48: 251–259.

Vepsäläinen, K. & Wuorenrinne, H. 1978: Ecological effects of urbanization on the mound-building *Formica* L. species. — *Memorabilia Zoologica* 29: 191–202.

Vepsäläinen, K., Savolainen, R., Tiainen, J. & Vilén, J. 2000: Successional changes of ant assemblages: from virgin and ditched bogs to forests. — *Ann. Zool. Fennici* 37: 135–149.

Walsh, C. & Mac Nally, R. 2004: Hierarchical partitioning. — *The R Project for Statistical Computing*, available on the web at http://cran.r-project.org/.

Wellenstein, G. 1980: Auswirkung hügelbauender Waldameisen der *Formica rufa*-Gruppe auf forstschädliche Raupen und das Wachstum der Waldbäume [Effects of "bare-backed" ants of the *Formica rufa* group on forestry insect epidemics and the growth of forest trees]. — *Z. ang. Ent*. 89: 144–157. [In German with English summary].

Westman, C. J. 1991: Maaperä ja sen toiminta kasvualustana. — *Helsingin yliopiston metsänhoitotieteen laitoksen tiedonantoja* 67: 1–40.

Wuorenrinne, H. 1974: Suomen kekomuurahaisten (*Formica rufa* coll.) ekologiasta ja levinneisyydestä [About the distribution and ecology of *Formica rufa*-group in Finland]. — *Silva Fennica* 8: 205–214. [In Finnish with English summary].