Distribution of mound-building ant species (*Formica* spp., Hymenoptera) in Finland: preliminary results of a national survey

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In the first year's data of the 10th Finnish National Forest Inventory (2005–2008) 533 active and 178 abandoned ant mounds were found yielding 4.2 mounds ha⁻¹. We found 11 species: *Formica rufa*, *F. polyctena*, *F. aquilonia*, *F. lugubris*, *F. pratensis*, *F. exsecta*, *F. fennica*, *F. pressilabris*, *F. forsslundi*, *F. suecica* and *F. uralensis*. Five species occurred throughout the country, and four were restricted to the south. We found species-specific associations with either mineral soils or mires, with forest site type and with tree-canopy openness. Low fertility decreased the occurrence of polygynous species with large worker force, and sun-exposition was favourable for species with smaller colonies presumably because only large worker force enables metabolic thermoregulation of nests. Forest fragmentation and increased amount of edge habitats favourable for colony founding have presumably increased nest density whereas drainage of mires has reduced the amount of habitat of three species since the 1950s.

Introduction

Mound building ants of the genus *Formica* have received a lot of attention owing to their great abundance in boreal forests and, especially in the wood ant group (*F. rufa* group), because of the multitude and magnitude of their ecological impacts. For instance, they affect the abundance and distribution of many forest-dwelling invertebrates (e.g. Savolainen & Vepsäläinen 1988, Niemelä *et al.* 1992, Way & Khoo 1992, Karhu & Neuvonen 1998, Laakso & Setälä 2000, Martikainen *et al.* 2000, Sipura 2002, Punttila *et al.*

2004) and vertebrates (e.g. Haemig 1992, 1994, Aho *et al.* 1999, Jäntti *et al.* 2007) in all forest layers from the forest soil and floor up to the tree trunks and canopies. Further, they are important resource for both invertebrates and vertebrates (e.g. Lehtinen 1987, Gösswald 1990, Elgmork & Kaasa 1992, Swenson *et al.* 1999, Päivinen *et al.* 2002), they play an important role in soil bioturbation (e.g. Pokarzhevskij 1981), in cycling and relocating carbon and nutrients (e.g. Lenoir *et al.* 2001, Kilpeläinen *et al.* 2007), in plant dispersal (e.g. Buckley 1982a, 1982b, Hölldobler & Wilson 1990) and, through their involve-

ment in mutualism with sap-sucking aphids and preying upon leaf-chewing insects, they apparently affect tree growth and plant production (e.g. Wellenstein 1980, Rosengren & Sundström 1991, Mahdi & Whittaker 1993, Atlegrim 2005). All these effects become reinforced and take effect on a larger spatial scale in polygynous colonies capable of forming multinest colonies. In Finland, the magnitude of these effects culminates in the top competitor *F. aquilonia* (e.g. Punttila *et al.* 1994, Punttila 1996 and references therein).

So far, however, systematic large-scale surveys of the distribution of different ant species are rare and they have concentrated mostly on the wood ant group (Burzyński 1969, Pileckis & Vilkauskas 1973, Seifert 1991). In the 10th Finnish National Forest Inventory (NFI10, 2005–2008), more than 10 000 sample plots (~0.05 ha each) are surveyed for mound-building ants. Here we report preliminary results based on the first year's data. These data serve in updating the distribution maps of the species: previously only coarse-scale distribution maps have been available (e.g. Baroni Urbani & Collingwood 1977, Collingwood 1979, Czechowski *et al.* 2002). Additionally, the data offer an opportunity to estimate the abundance distribution among species. This is not the first national ant survey in boreal countries, however, but the earlier surveys in Finland (NFI3, 1951–1953, *see* Wuorenrinne 1974, Rosengren *et al.* 1979, Kilpeläinen *et al.* 2005) and Sweden (in 2000s, *see* Kilpeläinen *et al.* 2005: 255) did not include species identification in the records of ant mounds (for the limitations of such an approach, *see* Kilpeläinen *et al.* 2005).

Here we present some general results on the occurrence of different ant species in relation to the major ecological gradients of boreal forests in Finland: forest vegetation zones (geographic area), soil type (mineral soil *vs*. mires), fertility (poor *vs*. fertile forest site types) and successional stage (open *vs*. closed tree canopy). Specifically, we explore whether the main patterns found in NFI3 ant mound data still hold when information about the ant species and colony vitality are taken into account. In the NFI3 data, mound occurrence decreased towards the north and was higher at fertile than at poor sites, and

higher in older than in younger forest development classes (Kilpeläinen *et al.* 2005). Further, because our myrmecological knowledge about mires is much more limited than that about mineral soils (in NFI3, only data for mineral soils were analyzed), and because also our knowledge of the effects of mire drainage for forestry purposes is much less than of the effects of forest management (e.g. clearcutting), we compared whether the occurrences of ant species differed between drained and undrained mires.

These data allow us also to test hypotheses which predict the occurrence of wood-ant species with different social strategies in relation to stand age and disturbance regime of the forest type (*see* Punttila 1996). Specifically we test the hypotheses that (1) monogynous wood ant species should be more common in young successional stages before the tree canopy closure whereas polygynous wood ant species should be more common in mature, closed canopy forests, and that (2) the monogynous strategy should be favoured in pine dominated forests on poorer soils which at the 1990s (*see* Discussion) were presumed to be subject to more frequent disturbances by wildfire than spruce forests on more fertile soils.

Material and methods

NFI produces information on forest resources and state of forests (for details, *see* Korhonen *et al.* 2006, 2007). In the field sampling a systematic grid of clusters of sample plots is laid over the entire country. The parameters of cluster sampling vary in different parts of the country according to spatial variation of forests. In field measurements, both forest-stand and individual-tree characteristics are described. For the forest stand where a sample plot is located, more than 100 variables are observed to describe the site, growing stock, damages and need for silvicultural operations. The tree data are used for estimation of volume and increment of growing stock. The sample plot size differs slightly between southern and northern Finland (*see* below) because the sampling criteria for trees measured differ between southern and northern parts of the country.

The ant nests were mapped on permanent circular sample plots of the NFI10. The radius of sample plots was 12.52 m in southern Finland (i.e. the two southernmost sampling areas below), and 12.45 m in northern Finland and thus, the plot size was a little smaller than 0.05 ha. In cases where the sample plot covered more than one stand, the ant sampling was restricted to the centre stand (the stand where the plot centre was located) resulting into reduced plot size. The size of such reduced plots was recorded in 10% classes of the whole sample plot. The majority of the ant mound plots, however, covered the whole sample plot (66% of all plots) or at least 90% of it (75%). All the mound density calculations are based on the exact area of the sample plots (also in the case of "reduced plot size" when the sample plot included stand edge(s)) in our analyses. All the plots are included in the frequency calculations. When calculating country-wise nest density estimates, the differing density of sampling plots in the four sampling areas (*see* below) was taken into account by using the forest and scrub land area represented by each of the sampling networks as a weight.

The ant mounds were inventoried on forest land (where the capability of producing volume increment is at least 1.0 m^3 ha^{-1} yr^{-1}) and scrub land (where the capability of producing volume increment is at least 0.1 m^3 ha^{-1} yr^{-1}) but not on wasteland (capability lower). Forest and scrub land cover 87% of all forestry land and 75% of total land area of Finland (Korhonen *et al.* 2006). The number of sample plots totaled 4150 in the first inventory year 2005. The sampling covered 40% of the permanent plots in the south, and 25% in the north. The sample plots were distributed as follows: Southern Finland (excluding Åland islands), 1448 plots, Middle Finland, 1704 plots, Northern Ostrobothnia-Kainuu (excluding Kuusamo area), 607 plots, and Lapland-Kuusamo (excluding northernmost Lapland), 391 plots (Fig. 1).

All ant mound nests exceeding 10 cm in height were included in the study when the apex of the mound situated on the sample plot (or, on the centre stand in the case of reduced ant sampling plots, *see* above), and the exact location in relation to the midpoint of the plot was recorded for each mound. The mounds were classified as
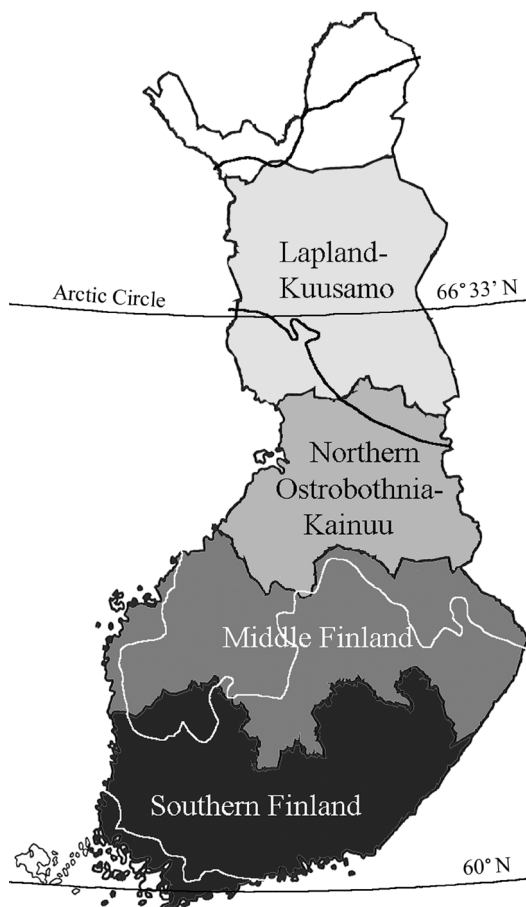

Fig. 1. The four sampling areas and their relation to the forest vegetation zones (hemi-, south-, mid- and north-boreal zones (simplified from Kalela 1960, and Ahti *et al.* 1968).

abandoned or active, and their appearance was recorded as intact, disturbed (by man [forestry operations] or other mammals or woodpeckers [predation; the mound dimensions were still measurable]), or broken (the dimensions were not measurable). For each mound, two measurements of diameter were taken: the largest possible and the one rectangular to the largest diameter. The possible "dead" parts (decayed, over-grown by vascular plants, not under active construction by the ants) in the lower sections of the mounds were included in the diameter. Also the mean height (above the forest floor level) of each mound was measured. All the measurements were recorded with 1 cm accuracy. Above-ground ant mound volumes were calculated with the half ellipsoid equation (*see* e.g.

Risch *et al.* 2005). Mound dimensions are commonly used as surrogates for worker population size of the mounds (e.g. Seifert 1991, Deslippe & Savolainen 1994, Liautard *et al.* 2003, Sorvari & Hakkarainen 2005). We used mound dimensions also when calculating nest density estimates to be compared with those in a recent Swedish inventory: only active colonies with minimum height of 20 cm and minimum width of 30 cm were taken into account in the Swedish inventory (G. Kempe pers. comm.).

For the present preliminary analyses, we selected four stand characteristics classified in rough categories which, however, reflect the most important ecological gradients in Finnish forests: forest vegetation zones (*see* Ahti *et al.* 1968, the four sampling areas approximated roughly the boreal zones along south–north gradient), soil type (mineral soils *vs.* mires), fertility (poor *vs.* fertile, i.e. *Vaccinium* site type and poorer stands *vs.* *Myrtillus* site type and richer stands — for the site types, *see* Cajander 1949), and successional stage of the stand (open *vs.* closed canopy; tree-canopy cover less than or equal to 40% *vs.* more than 40%). For ants, one of the most important habitat characteristics changing during forest succession is exposition to sun. Because sun exposition varies a lot with several stand characteristics (e.g. tree species composition and site type of the stand) in addition to successional stage or age of the stand, we selected tree canopy cover to approximate successional stage in our analyses. Additionally, we compared whether the occurrences of ant species differed between drained and undrained mires. We utilized the NFI classes based on the effects of ditching ("drainage succession"): drained mires are classified into recently drained mires, transforming mires and transformed mires. During drainage succession water level decreases and the growth of the tree stand accelerates.

For each active ant mound, a sample of about 20 worker ants was taken and stored in ethanol, and the samples were identified to species in the laboratory. Owing to commonly found difficulties in the identification of mound-building *Formica*, we consulted several identification keys and research papers (especially those dealing with chaetotaxonomy of the wood ant species) during the identification process (e.g. Dłussky

& Pisarski 1971, Collingwood 1979, Douwes 1979, 1981a, 1981b, 1995, Vepsäläinen & Pisarski 1981, Seifert 1991, 1996a, 1996b, 2000, 2003, Czechowski & Douwes 1996, Czechowski *et al.* 2002, Goropashnaya *et al.* 2004a, 2004b, Sorvari 2006).

We used log-likelihood ratio test (G^2) to evaluate whether the occurrence of species depended differently on environmental variables and also to evaluate whether the relationship was the same between abandoned and active ant mounds. When statistically significant relationships were found, we explored the cell contributions (observed–expected) to the test statistics to aid the interpretation of the test results. These analyses were performed with Statistix software, ver. 8 (Analytical Software, Tallahassee, Florida, USA).

Results

The first year's survey yielded a total of 533 active ant mounds (includes five mounds with missing location data because of incomplete sample labeling), and 178 abandoned mounds. Thus, 25% of all mounds were abandoned. Most of the sample plots (86.3%) housed no ant mounds, and only 2.4% of the plots had more than one mound. The samples represented 14 ant species of all the four subgenera of *Formica* found in Finland (Table 1). Eleven of these species were truly mound-building ones: five species of wood ants of *Formica rufa* group (*F. rufa*, *F. polyctena*, *F. aquilonia*, *F. lugubris* and *F. pratensis*), five species of *Coptoformica* (*F. exsecta*, *F. fennica*, *F. pressilabris*, *F. forsslundi* and *F. suecica*), and *Formica uralensis*. Additionally, some atypically large nests of other *Formica* species were found in the survey (*Formica truncorum*, *F. sanguinea*, and *F. picea* — especially the latter one, however, was evidently accidental in the samples and it was presumably housing an abandoned mound built by some other species). The distributions of the latter three species are not analyzed here because the sampling procedure heavily underestimates their occurrence. However, the present data probably reflect their overall distribution given that small and large colonies are distributed approximately similarly. The most common species were *F. aquilonia*

(57% of all samples), *F. exsecta* (14%) and *F. lugubris* (11%), and *F. rufa*, *F. uralensis* and *F. polyctena* comprised 2%–3% each (Table 1).

The biggest mounds were found in the wood ant group, where the largest average sizes were recorded in the polygynous species *F. polyctena* and *F. aquilonia*, 1.0 and 0.5 m³, respectively, whereas the average size was smaller in the monogynous wood ant species (*F. lugubris*, *F. rufa* and *F. pratensis*, 0.1–0.4 m³, Table 1). Similarly, the mounds of *F. exsecta* and *F. fennica* were five times larger than those of the rest of the *Coptoformica* species (Table 1). The biggest mound in these data was 6.6 m³ and it was inhabited by *F. aquilonia*.

The overall density of ant mounds (all species and active and abandoned mounds pooled) was on average 4.2 (± 0.44 SE) mounds ha⁻¹. Because the reduction in sample plot size may

lead to boosted mound densities due to edge effects (*see* Discussion below), we examined how the size of the ant mound recording plot (the 10% size classes of the centre stand's proportion of the full ~0.05 ha sampling plot) affected the density estimate. In the smallest size classes (10%–40%), the number of plots was extremely low (1–20 plots) and thus, these plots yielded hardly any ant mound observations. With 50% plot size, however, the number of plots was already reasonable and ant mounds were encountered more often. This resulted in very high density estimate and large variation, i.e. 9.1 (± 1.93 SE, based on 116 plots) mounds per ha (Fig. 2). The density estimate and its variation became lower with increasing plot size and increasing number of plots per size class (Fig. 2). With full 100% (~0.05 ha) sample plots, the average was 3.3 (± 0.19 SE) mounds per ha (Fig. 2).

Table 1. Ant mound observations and mound characteristics (height, width, volume and density; for density, all the sample plots were used — *see* text) in the 4150 sample plots of NFI10 (2005), and the share of each species.

Species	Subgenus[1]	Height (m)		Width (m)		Volume (m³)		Density (ha⁻¹)		Tot.	%
		Mean	SE	Mean	SE	Mean	SE	Mean	SE		
Formica aquilonia	Fw	0.53	0.02	1.00	0.03	0.52	0.05	1.60	0.24	302	56.7
Formica exsecta	C	0.33	0.01	0.52	0.02	0.06	0.01	0.52	0.16	76	14.3
Formica lugubris	Fw	0.45	0.03	0.81	0.06	0.25	0.04	0.41	0.12	58	10.9
Formica rufa	Fw	0.49	0.06	1.02	0.13	0.40	0.11	0.06	0.02	15	2.8
Formica uralensis	F	0.25	0.04	0.49	0.08	0.06	0.03	0.10	0.05	15	2.8
Formica sanguinea	R	0.22	0.03	0.55	0.03	0.04	0.01	0.09	0.06	14	2.6
Formica truncorum	F	0.31	0.04	0.70	0.08	0.11	0.04	0.12	0.06	13	2.4
Formica polyctena	Fw	0.73	0.11	1.33	0.16	1.01	0.46	0.09	0.05	12	2.3
Formica fennica	C	0.36	0.07	0.50	0.04	0.06	0.02	0.10	0.06	8	1.5
Formica pressilabris	C	0.21	0.02	0.35	0.04	0.01	0.00	0.03	0.01	6	1.1
Formica forsslundi	C	0.17	0.04	0.29	0.05	0.01	0.00	0.02	0.02	4	0.8
Formica pratensis	Fw	0.17	0.09	0.60	0.45	0.07	0.07	0.01	0.00	2	0.4
Formica suecica	C	0.17	0.02	0.36	0.01	0.01	0.00	0.01	0.01	2	0.4
Formica picea	S	0.15	–	0.38	–	0.01	–	–	–	1	0.2
Missing data[2]	–	–	–	–	–	–	–	–	–	5	0.9
Active mounds, all spp.		0.47	0.01	0.86	0.02	0.38	0.03	3.19	0.35	533	100.0
Abandoned mounds		0.40	0.02	0.91	0.04	0.35	0.04	1.06	0.20	178	
All mounds (abandoned and active)		0.45	0.01	0.87	0.02	0.37	0.03	4.25	0.44	711	

[1] Abbreviations for subgenera: F = *Formica s. str.*, C = *Coptoformica*, R = *Raptiformica*, and S = *Serviformica*; w = the species belongs to the wood ant group (*F. rufa* group).
[2] Missing data includes five ant samples identified to species (*F. aquilonia*, *F. exsecta*, *F. lugubris*, *F. sanguinea* and *F. forsslundi*, one sample of each species) for which no mound or plot data was available because of incomplete sample labeling. These data were omitted from all the species specific analyses.
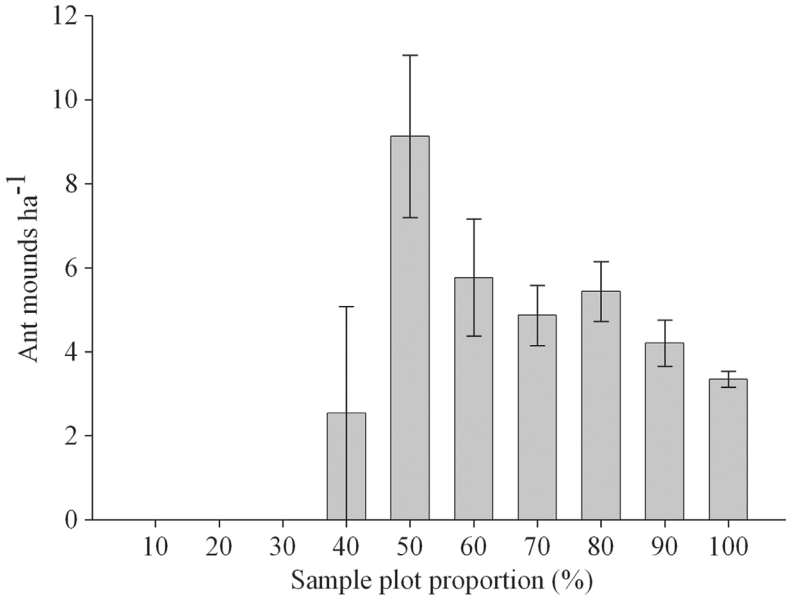
Fig. 2. Ant mound density in relation to the proportion of sample plot to the full sample plot.
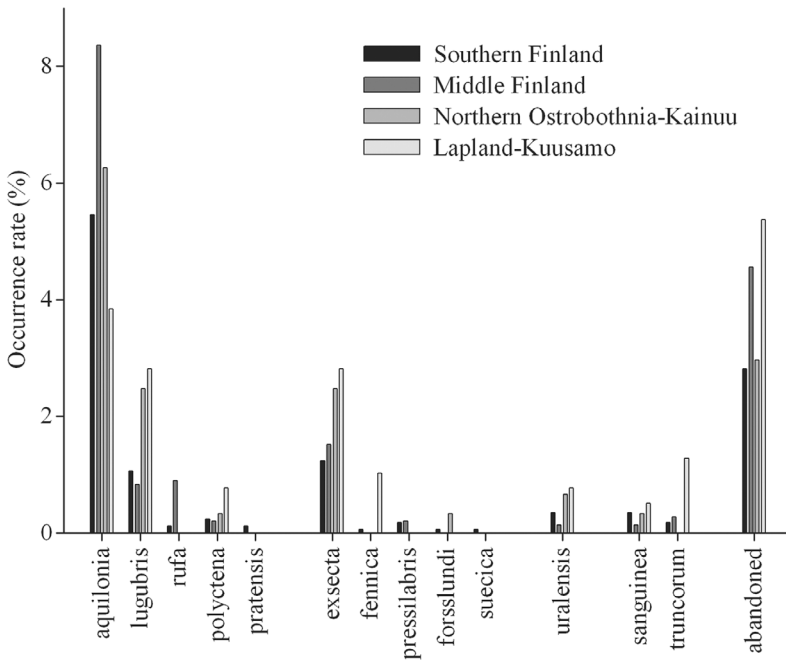

Fig. 3. The occurrence rate (% of sample plots) of mounds of different ant species and abandoned mounds in different sampling areas.

Overall, five mound-building species (*F. polyctena*, *F. aquilonia*, *F. lugubris*, *F. exsecta* and *F. uralensis*) occurred throughout the country, and four species (*F. rufa*, *F. pratensis*, *F. pressilabris*, and *F. suecica*) were restricted to southern parts of the country (Fig. 3). The distribution of species occurrences in relation to geographic area was clear (pooled sampling areas

southern *vs.* northern Finland; $G^2 = 61.03$, df = $10, p < 0.001$): *F. aquilonia* and *F. rufa* were less and *F. exsecta*, *F. fennica* and *F. lugubris* were more frequent in the north than expected.

Although the three most common species were the same on mineral soils and mires, all the species except *F. lugubris* showed quite clear association with either of the habitat types (min-
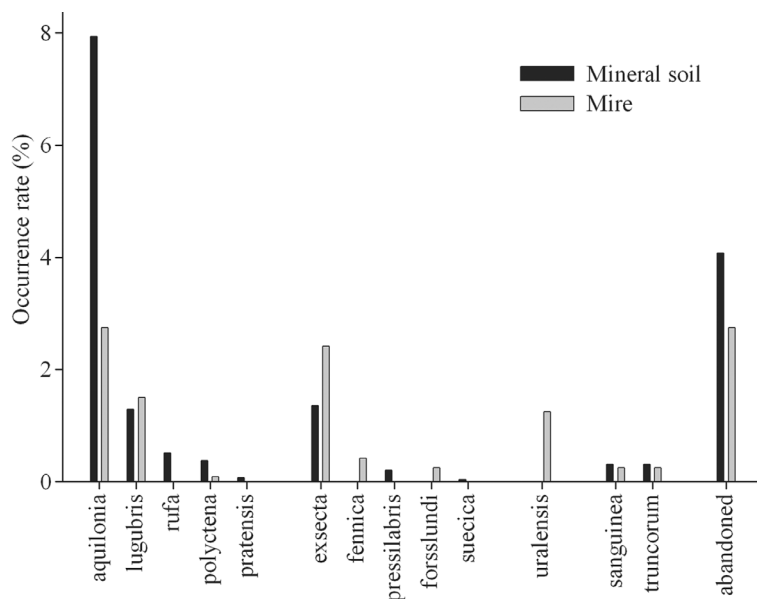
Fig. 4. The occurrence rate (% of sample plots) of mounds of different ant species and abandoned mounds on different soil types.

eral soils: *F. rufa*, *F. polyctena*, *F. aquilonia*, *F. pratensis*, *F. pressilabris*, *F. suecica*; mires: *F. exsecta*, *F. fennica*, *F. forsslundi* and *F. uralensis*; Fig. 4). The distribution of ant species occurrences differed clearly in relation to the habitat type (mineral soils *vs.* mires): *F. aquilonia* was less and *F. uralensis*, *F. exsecta*, *F. fennica* and *F. forsslundi* were more frequent on mires than expected ($G^2 = 143.12$, df = 10, $p < 0.001$). The overall density of ant mounds on mineral soils and mires was on average 4.4 (± 0.23 SE) and 3.1 (± 0.31) mounds per ha, respectively. With full 100% sample plots, the respective densities were 3.5 (± 0.22) and 3.0 (± 0.37) mounds per ha. The density estimates comparable with those of the recent Swedish inventory (*see* Material and methods) were 2.6 (± 0.16) and 1.8 (± 0.21) mounds ha⁻¹ on mineral soils and mires, respectively.

The three species confined exclusively to mires, *F. uralensis*, *F. fennica* and *F. forsslundi*, occurred less frequently on drained mires than on undrained ones and further, their occurrence rate decreased with drainage succession, and the occurrence of abandoned mounds peaked in recently drained and transforming mires (Fig. 5). All the three species were absent from mineral soils. The only frequent species on mires that, however, was associated with mineral soils, *F. aquilonia*, seemed to have been benefited from

draining (Fig. 5). The distribution of ant species occurrences differed clearly in relation to drainage classes (undrained *vs.* recently drained and transforming *vs.* transformed: $G^2 = 31.80$, df = 12, $p = 0.002$): *F. aquilonia* was more common on transformed mires, and *F. fennica* and *F. uralensis* were more frequent in undrained mires than expected.

Only *F. aquilonia* occurred more often under closed tree canopy than in open conditions. With two exceptions, *F. rufa* and *F. polyctena* which occurred at similar frequencies under open and closed canopy, all the rest of the species were associated with open tree canopy (Fig. 6). The distribution of ant species occurrences differed clearly in relation to canopy openness (tree-canopy cover less than or equal to 40% *vs.* more than 40%: $G^2 = 63.61$, df = 10, $p < 0.001$): *F. aquilonia* was less and *F. exsecta*, *F. fennica* and *F. uralensis* were more frequent in open canopy stands than expected.

The polygynous wood ants, *F. aquilonia* and *F. polyctena* occurred more frequently on fertile than poor mineral soils and mires, whereas the opposite was true for most of the other species (Figs. 7 and 8). The distribution of species occurrences in relation to site fertility (fertile *vs.* poor soils) did not differ on mires ($G^2 = 11.26$, df = 6, $p = 0.081$; *F. aquilonia* was slightly more and *F. forsslundi* slightly less frequent on fertile mires
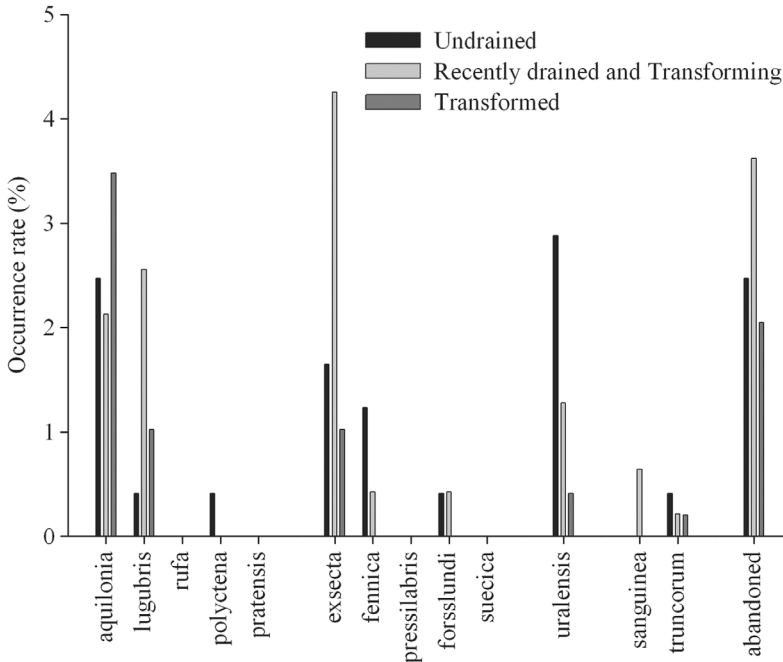
Fig. 5. The occurrence rate (% of sample plots) of mounds of different ant species and abandoned mounds on mires in relation to drainage classes.
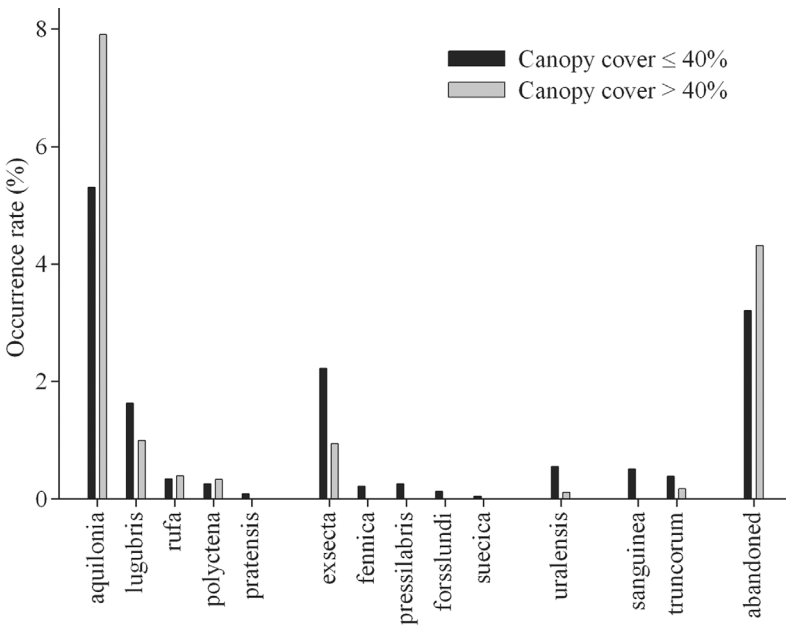

Fig. 6. The occurrence rate (% of sample plots) of mounds of different ant species and abandoned mounds in relation to the tree-canopy cover.

than expected but not statistically significantly so). On mineral soils, however, the distribution of species in relation to fertility differed clearly (fertile *vs.* poor soils: $G^2 = 45.91$, df = 7, $p < 0.001$): *F. aquilonia* was less and *F. lugubris*, *F. rufa* and *F. suecica* were more frequent on poor sites than expected.

The distribution of active *vs.* abandoned mounds was the same in relation to geographic area (the two southernmost sampling areas *vs.* the two northernmost areas pooled: $G^2 = 0.64$, df = 1, $p = 0.424$). Similarly, the distribution of active *vs.* abandoned mounds was the same also in relation to habitat type (mineral soils
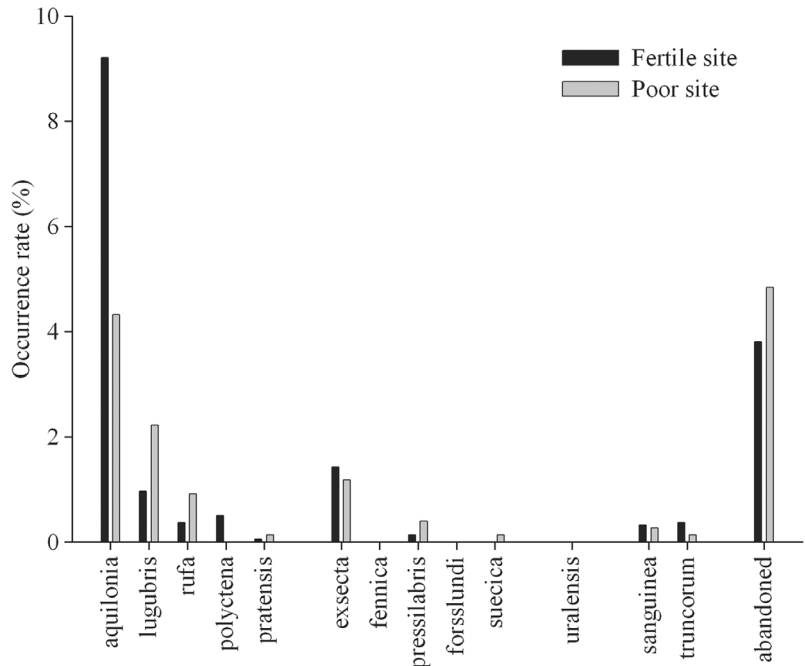
Fig. 7. The occurrence rate (% of sample plots) of mounds of different ant species and abandoned mounds in relation to the site fertility on mineral soils.
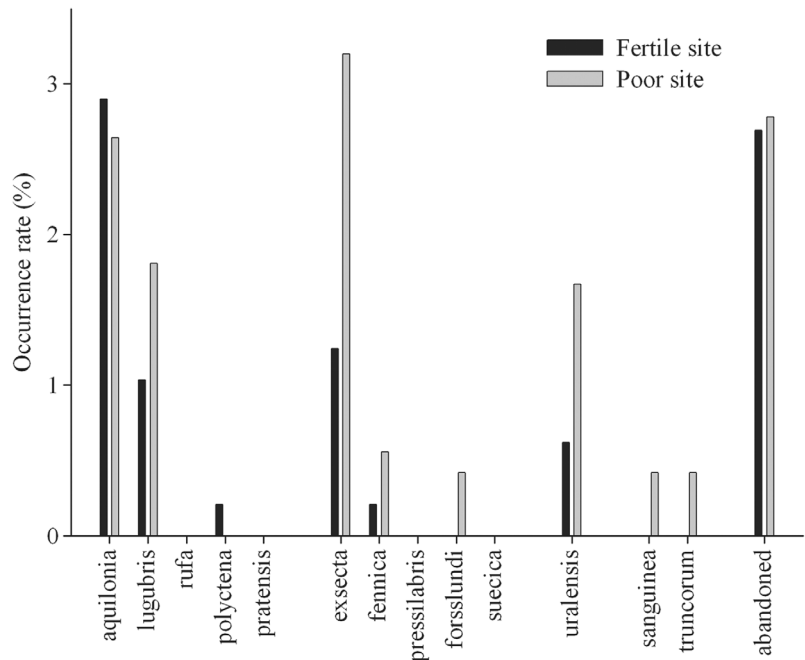

Fig. 8. The occurrence rate (% of sample plots) of mounds of different ant species and abandoned mounds in relation to the site fertility on mires.

vs. mires: $G^2 = 0.37$, df = 1, $p = 0.541$), to mire drainage classes (undrained *vs.* recently drained and transforming *vs.* transformed: $G^2 = 0.19$, df = 2, $p = 0.908$), and to canopy cover ($\leq 40\%$ *vs.* > 40%: $G^2 = 2.86$, df = 1, $p = 0.091$; abandoned mounds were slightly more frequent in closed canopy forests than expected but not statistically significantly so). The distribution of active *vs.* abandoned mounds was the same in fertile and poor mires (fertile *vs.* poor soil: $G^2 = 1.77$, df = 1, $p = 0.184$), but on mineral soils abandoned mounds were more frequent on poor sites than expected ($G^2 = 7.37$, df = 1, $p = 0.007$).

Discussion

Inclusion of species identification and information about e.g. colony vitality in the 10th Finnish National Forest Inventory made it possible to analyze mound data in much more detail than in the previous third inventory, and the analyzes revealed several new patterns of species distribution in Finland. Generally, our results verified most of the main patterns found in NFI3 (1951–1953) ant mound data (Wuorenrinne 1974, Rosengren *et al.* 1979, Kilpeläinen *et al.* 2005) where no information was available for ant species, mound size nor colony vitality: mound occurrence decreased towards the north (Fig. 3) and was higher on fertile than on poor sites (Fig. 7). Mound occurrence, however, did not depend on canopy openness in NFI10 data (Fig. 6) — canopy openness approximates early and more advanced development classes among which there were differences in the NFI3 data.

Mound density, vitality and size

On mineral soils, the overall density of ant mounds (all species and active and abandoned mounds pooled) may have increased from that at the time of NFI3 (2.5 mounds per ha, *see* Kilpeläinen *et al.* 2005) to 3.5 or 4.4 mounds per ha (based on full or all sample plots, respectively), and it seemed to be quite similar to that found in a recent national survey in Sweden: for large active mounds, the density was 2.6 and 2.2 mounds ha⁻¹ in our data and Sweden, respectively (G. Kempe pers. comm. for the Swedish data).

It is likely that ant mound density has increased from the 1950s because of the drastic management induced changes in landscape and stand structure since that time (Punttila *et al.* 2005): most importantly, forest fragmentation has diminished the average stand size remarkably and thus increased the proportion of edge habitats (e.g. Wuorenrinne 1983, 1989, Löfman & Kouki 2001, 2003). The effect of edge habitats was very clear in the present data. In the sample plots where the ant sample plot size was reduced, always more than one forest stand was included in the full plot area and thus, these plots were located in various kinds of stand edges. When the size of the ant-sampling plot was reduced to 50% from the full ~0.05 ha size, the density estimate of mounds increased almost three-fold (Fig. 2). Edge effect explains the high mound density as most forest dwelling mound building ant species favour edge habitats in colony founding (Punttila 1996, Sorvari & Hakkarainen 2005, Kilpeläinen *et al.* 2008).

The written instructions for the NFI3 did not contain any minimum size for ant mounds to be counted nor any information whether only active or both active and abandoned mounds were counted and thus, direct comparisons between these two inventories (NFI3 and 10) cannot be reliably done. In the present data, for instance, the density estimate increased from 2.6 to 4.4 mounds ha⁻¹ on mineral soils when also small ($h > 10$ cm) and abandoned mounds were included in addition to active and larger ($h \geq 20$ cm) mounds. This is because small mounds with higher mortality may be very common in certain habitats and successional stages.

Abandoned mounds comprised about 10%–16% of all mounds in previous studies on fertile (mesic *Myrtillus* type) and medium rich (*Vaccinium–Myrtillus* type) stands of different age on mineral soils (considering only true mound building species, Punttila 1996, Domisch *et al.* 2005, Kilpeläinen *et al.* 2008), but our data showed a higher proportion (25%) of abandoned mounds probably because also less favourable site types were included.

Our results on mound sizes verified the information available on relative mound size differences among different species (cf. Collingwood 1979). We found that mounds of the polygynous species were remarkably larger than those of the monogynous ones especially in the wood ant group (Table 1). Although in our data the biggest individual mound, 6.6 m³, was inhabited by *F. aquilonia*, the average size was clearly highest in *F. polyctena*. All the giant mounds > 10 m³ studied in Finland have been reported to be inhabited by *F. polyctena* (*see* Wuorenrinne 1994).

Species distributions

The commonness of *F. aquilonia*, *F. exsecta* and

F. lugubris was verified in our data (Fig. 3): these species and *F. uralensis* are widespread also according to published broad-scale maps (*see* Baroni Urbani & Collingwood 1977, Collingwood 1979, Czechowski *et al*. 2002). The other similarly widespread species in our data, *F. sanguinea* and *F. truncorum*, however, do not commonly build mound-like large nests and thus, their commonness is severely underestimated in the present data. Similarly, *F. suecica* builds very small nests and thus, it is underrepresented in our data. Small nest size may explain also the apparent rarity of *F. pressilabris* and *F. forsslundi* in our data. Given the scarcity of occurrences of *F. suecica* and *F. forsslundi* in the distribution maps (Collingwood 1979, Czechowski *et al*. 2002), the few records of the species in the present data still indicate that these species may be much more common than earlier thought. The recently described *Coptoformica* species *F. fennica* (Seifert 2000) was found to be rather common in Finland: it was the second most common *Coptoformica* species in our data, and it was much more common in the north than in the south. Earlier it was known from a few locations in southern Finland. The scarcity of *F. rufa, F. pratensis* and *F. pressilabris* may partly owe to their southern distribution but unlike sometimes thought (e.g. Baroni Urbani & Collingwood 1977, Collingwood 1979, but *see* Czechowski *et al*. 2002), *F. polyctena* was not restricted to the southern part of the country. Instead, it seemed to be more common in the north than in the south, while we found an opposite pattern in the other polygynous wood ant species, *F. aquilonia*. Different wood ant species have monopolized the polygynous "niche" in different parts of Europe (Rosengren *et al*. 1993), and also in the present case the lower frequency of the most potential competitor, *F. aquilonia* and most of the other species may have enhanced the spread of polygynous *F. polyctena* in the north. Similarly, *F. lugubris*, *F. exsecta* and *F. uralensis* may have gained habitat in the north because of the low frequency of *F. aquilonia* there. Especially *F. uralensis* has been suggested to be a weak competitor which may be suppressed by the stronger species (Rosengren 1969, Collingwood 1979).

Habitat associations

Previously mainly qualitative information has been available on the distribution of species between the main habitat types, mineral soils and mires (Collingwood 1976, 1979, 1999, Vepsäläinen *et al*. 2000). Our data showed that although the three most common species were the same in these habitat types, most of the species showed a clear association with either of the main habitats, and three species were confined to mires (Fig. 4). Perhaps the most interesting finding was that *F. fennica* occurred exclusively on mires: this species has been reported to inhabit grasslands (Seifert 2000). Treeless grasslands, however, were not included in our ant sampling. Large proportion of mires has been drained in Finland to enhance forest growth: the proportion of drained mires is about 40% in the two northernmost provinces (Oulu and Lapland, i.e. the two northernmost sampling areas and northernmost Lapland in Fig. 1, the area above ca. the latitude 64°N) and about 80% in the southern provinces (Auvinen *et al*. 2005). The drainage started on a large scale in the 1950s when still about 80% of the mires in the southern Finland were undrained (Auvinen *et al*. 2005). We showed that drainage causes rapid disappearance of mound building mire ant species (*see* also Collingwood 1999, Vepsäläinen *et al*. 2000) which suggests that their populations have declined remarkably especially in the southern Finland since the 1950s (Fig. 5). In our data, three species, *F. uralensis*, *F. fennica* and *F. forsslundi*, showed a clear negative trend in their occurrence rate with time since ditching, while the opposite was found in *F. aquilonia* that was associated with mineral soils. The greater abundance of undrained mire habitats in the north may partly explain why *F. exsecta*, *F. fennica*, *F. forsslundi* and *F. uralensis* were more frequent there than in the south.

Punttila (1996) hypothesized that monogynous wood ant species should be more common in young successional stages before the tree canopy closure whereas polygynous wood ant species should be more common in mature, closed canopy forests. In our analyses, we used the cutpoint of 40% tree canopy cover to roughly separate open (or younger) and closed (or older) forests. Although the distribution of the two

most common wood ant species, polygynous *F. aquilonia* and monogynous *F. lugubris*, was in accordance with the hypothesis, the data on the less frequent species may be too scanty to draw any conclusions on this matter (Fig. 6). All the other territorial species (other than the species of the wood ant group) were associated with open tree canopy which has been the case in previous studies as well (for discussion on the role of these species in ant community succession, *see* Punttila 1996, Punttila *et al.* 1996).

The distribution of active and abandoned mounds differed from each other between fertile and poor mineral soils (Fig. 7) but not between fertile and poor mires (Fig. 8). Presumably this indicates higher turnover rate of ant colonies on poor mineral soils, where monogynous species (*F. lugubris*, *F. rufa* and *F. pratensis* of the wood ant group) were much more common and polygynous species (*F. aquilonia* and *F. polyctena* of the wood ant group) much less common than on fertile soils. Life span is shorter in monogynous colonies whereas polygynous colonies may theoretically be everlasting because of continuous recruitment of new queens and support from the multinest network. On mires, polygynous strategy prevails also on poor types: some of the most frequent species were polygynous ones (e.g. *F. exsecta* and *F. uralensis*, Fig. 4) which may explain why the turnover rate, as indicated by the frequency of abandoned mounds in relation to active ones, did not differ between poor and fertile mires similarly as between poor and fertile mineral soils.

Disturbance frequency *vs.* habitat type

Punttila (1996) hypothesized that the monogynous strategy should be favoured on pine dominated forests on poorer soils which at that time were presumed naturally to be subject to more frequent disturbances by wildfire than spruce forests on more fertile soils. Indeed, for the last 500 years, the fire frequency has been shown to have been higher in pine dominated forests than in spruce dominated ones (Zackrisson 1977, Engelmark 1987, Wallenius *et al.* 2004). Since then, however, it has been shown that the fire-return interval before increased human impact

also in pine dominated forests in addition to spruce dominated ones has been much longer than generally believed at the time when only short dendrochronologies (< 500 yrs) were available although the frequency may have differed among the site types (*see* Pitkänen *et al.* 2002, 2003a, 2003b, Wallenius 2002, Wallenius *et al.* 2004, 2005). We evaluate the hypothesis of Punttila (1996) under the light of these new findings below.

Under natural conditions fire frequencies in general were low and thus, the monogynous strategy might be viewed as an pre-adaptation to human induced elevated fire frequency rather than as an adaptation to naturally high disturbance frequency as such. As forest fires on all forest site types have been efficiently prevented for decades and natural disturbances (storms, fires, floods, insect outbreaks, etc.) leading to forest regeneration have been replaced with thinning and regeneration cuttings (clearcutting), and rotation cycles of managed forests on poor soils are generally longer than on fertile soils (e.g. according to the present forest management guidelines 70–90 years on fertile and 80–120 years on poor soils in Southern Finland, *see* Metsätalouden kehittämiskeskus Tapio 2006: p. 34), we should not expect us to find disturbance related distribution patterns in the sense of the hypothesis of Punttila (1996). Our data showed that the monogynous wood ant species were more frequent and polygynous ones less frequent on poor mineral soils than on fertile soils (Fig. 7) just as predicted by the hypothesis (Punttila 1996). The most likely explanation for this may, however, not be the higher disturbance frequency on these soils but rather the low fertility and open tree-canopy cover of these forests as such. Open tree canopy cover is favourable for colony founding in mound building ants in general. Low fertility, on the other hand, may also indicate low amounts of resources for wood ants and thus, we expect smaller colony population size in ant mounds on poor soils. Both low site fertility and monogynous strategy associate with small colony population size. A small colony population remain dependent on direct sunlight during the whole colony cycle to be able to reach and maintain sufficient intracolony temperature. This is because mere metabolic

heat production by small worker force does not allow thermoregulation independent from sun exposition unlike in the abundantly populated mounds of the polygynous wood ant species (*see* Rosengren *et al.* 1987). The preconditions for the success of the monogynous strategy in wood ants are met on poor soils where the tree canopy of pine dominated forests remain relatively open throughout most of the successional cycle. The above disturbance and habitat hypotheses, however, do not exclude but complement each other.

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