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Successional changes of ant assemblages: from virgin and ditched bogs to forests

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We studied ant assembly changes after ditching of bogs with nest and pitfall sampling in the southern Finnish taiga. The study sites clustered in dendrograms to hierarchical sets: virgin bogs and young ditchings, older ditchings, and forests. Species richness was low on virgin bogs and young ditchings, and increased with the age of ditching. The number of species was highest in clearcut, and decreased in spruce forests with increasing density of wood ants. Three bog specialists, *Formica uralensis*, *F. picea* and *Myrmica scabrinodis*, were found only on bogs. Nation-wide draining of bogs implies severe decreases in their population densities. As a corollary, the poorly known but potentially healthy populations of the obligate social parasite of *M. scabrinodis*, *Myrmica karavajevi*, may go extinct in extensive regions, because of its need of high nest densities of the host species. The effects of habitat attributes on the local number of species were overshadowed by top-dominant, polydomous wood ants. A wood with practically no *F. aquilonia* harboured 11 other ant species, whereas in high-density wood-ant forest only two other species were located. Pre-emption by the slave-maker *F. sanguinea* may in several ways slow down the spread of wood ants to ditched bogs.

1. Introduction

Successional changes of the environment are known to affect the structure of ant assemblages profoundly. Vepsäläinen and Pisarski (1982) outlined the successional changes of ant assemblages taking place during primary succession caused by land upheaval in an archipelago in the Baltic Sea. On the neighbouring mainland, Gallé (1991) analyzed ant assemblages of a coastal dune area. Punttila and coworkers (e.g., Punttila *et al.* 1991, Punttila 1996, Punttila *et al.* 1996) described changes during secondary succession after forest clearcuts in the Finnish taiga. These and other studies on the interrelations among ant species (Savolainen & Vepsäläinen 1988, 1989, Savolainen *et al*. 1989, Vepsäläinen & Savolainen 1990) show that succession of ant assemblages depends on ecological factors that limit nesting and foraging, the dispersal and colonization capacities of the species, and competition among the species.

Till the beginning of the 1980s, about half of the Finnish bogs had been ditched in order to improve local growth of trees, and ultimately afforest the bogs. In the southern half of Finland, the proportion of ditched bogs was 71% (Metsätilastollinen vuosikirja 1989). In spite of this large-scale human interference with the bog habitats, no studies on successional changes of bog insect assemblages have been published.

The aim of this study is to describe the structure of ant assemblages on bogs of different ditching ages, and to compare the assemblages to those on unditched patches of bogs and in neighbouring forests. We expect that the local ant assemblages are hierachically ordered in a sere which reflects the successional habitat changes from unditched bogs through younger and older ditchings toward forests. Specifically, we looked for ant species specialized in bogs, and their fate as a function of habitat change. We also studied the competitive impoverishment of ant assemblages caused by highly territorial, multinest societies of wood ants.

2. Study areas and sampling

The main study sites are located in Lammi commune, southern Finland (61°02´N, 24°58´E). The region is characterized by fairly small-scaled mosaic of bogs and spruce-dominated forest (mainly of the *Oxalis–Myrtillus* type of A. K. Cajander's (1949) forest classification) interspersed with old, fertile agricultural landscape. The bogs Laaviosuo and Kaurastensuo are separated from each other by a 300 m stretch of forest. Both are ombrotrophic eccentric raised bogs (Vasander 1982 and H. Vasander pers. comm.). Laaviosuo covers 64 ha, all of which has been ditched, but of the 92-ha Kaurastensuo 38 ha remains unditched. Another study bog (unditched Heinisuo) is a small kettlehole mire, located in the neighbouring commune Hämeenkoski, ca. 700 m farther SE. Table 1 summarizes the age of ditchings (if any), bog or forest types, and additional habitat attributes of the study sites.

The unditched areas of Kaurastensuo look mutually fairly similar to the eye of a myrmecologist, as do young, medium-aged and old ditched

Table 1. The studied bog patches (for mire classification, *see* Ruuhijärvi 1983). The age of ditching is given in years (complementary ditching in parentheses), and the average height of trees in metres. Trees are pine, at Heinisuo pine and birch sparsely mixed with spruce. Site codes: underlined = only pitfall-trapping (1980), normal = only search for nests (1978–1979), boldface = both hand- and pitfall-collecting (1998). The mnemonic site codes are based mainly on the habitat and age of ditching of the sites.

Site	Bog	Ditching (a)	Bog type	Trees (m)
H1	Heinisuo	Unditched	cottongrass pine bog	8–10
H2	Heinisuo	Unditched	oligotrophic sedge-pine mire	8–10
H3	Heinisuo	Unditched	mesotrophic sedge-pine mire	8–10
U/E	Kaurastensuo/E	Unditched	hummock-and-hollow pine bog	1–3
U/W	Kaurastensuo/W	Unditched	hummock-and-hollow pine bog	1–3
B1	Laaviosuo	0.5–1.5	hummock-and-hollow pine bog	1–3
B12	Laaviosuo	12–13	hummock-and-hollow pine bog	3–5
B20	Laaviosuo	20	transitional phase1)	4–6
B32	Laaviosuo	32 (20)	transitional phase1)	9–11
B35S	Kaurastensuo/S	35 (15)	transitional phase2)	12–13
B35N	Kaurastensuo/N	35 (15)	transformed phase3) (forest stage)	13–15

1) after ditching of hummock-and-hollow pine bog; 2) after ditching of dwarf-shrub pine bog; 3) after ditching of dwarf-shrub pine bog

patches, respectively. However, Heinisuo is a mosaic of different mire site types varying from ombrotrophic to eutrophic (Reinikainen *et al.* 1984). The studied mature, spruce-dominated shady forests have mutually similar vegetation, although part of the sites are affected by edges (Table 2). A clearcut was included to the study to hopefully obtain a site void of top-dominant, polydomous wood ants. Although originally a rich spruce-dominated forest, due to its open and exposed topography, it is now, as regards ants, probably closer to pine forests than to the rest of the studied forests. The scarcity of dry pine twigs and sticks on the ground renders, however, the clearcut qualitatively different from open pine forests, because decaying sticks of spruce and young deciduous trees are much less suitable as nest sites for *Leptothorax* species than are pine sticks.

Ants were collected (1) by hand, searching through possible places of ant nests; and (2) by pitfall trapping. The latter method is widely used in sampling insect communities, but it is deficient in ecological ant studies by ignoring species which live practically entirely underground. Although hand-collecting is more time-consuming and liable to individual differences among collectors with differing field experiences, the method supplements the results obtained by pitfall trapping. However, whereas hand-collecting renders data with a species-specific nest as an observation in the data, pitfalls include potentially many individuals of several species belonging to different unknown nests. This discrepancy in quality between the two collecting methods is insurmountable, and necessitates separate analyses of the two methodologically different data sets.

We started the study on Laaviosuo in the summer of 1978 with pioneer collectings within a bog patch ditched in the previous winter (B1 in Table 1), and within a 12 year-old ditching (B12). Sampling in these patches was carried on in 1979, and in 1980 three mutually clearly different bog habitats were studied in Heinisuo. In 1998, more collecting took place within Kaurastensuo and Laaviosuo in two unditched bog patches, and four ditchings of the age 20–35 years (the 1978–1979 sites were included in this set of study patches: B20 and B32 in Table 1). We also collected in a neighbouring wood of each of the six bog study sites, and in one four years old clear-cut forest area (Table 2). All the study sites in Lammi are located within the northwestern half of the circle with a radius of one km, drawn from within the 10 × 10 m square 677070:339143 in the Finnish Uniform Grid 27°E.

In 1978–1979 ants were collected by hand at sites B1 and B12, where three and four study lines of 100–210 m, respectively, were drawn from the bog edge into the bog; the breadth of each studied transect was two metres. In 1978 in site B1, a 180 m transect was run along the fresh ridge of wet dug-up turf alongside a ditch; because no ant nests were found there, the transect was omitted from the data. Consequently, 1978–1979 produced data from an area of ca. 840 m^2 and 1 400 m^2 in sites B1 and B12, respectively.

Table 2. The studied forest sites (for type classification, *see* Cajander 1949). The location of the patch is given relative to the neighbouring bog patch (in parentheses). Spruce-forest patches studied in 1998 (S1–S6) are given in order of increasing density of *Formica aquilonia*. Site S/79 only searched for nests (1979), in other sites both hand- and pitfall-collecting (1998). Notes indicate presence or closeness of edges because of road or clearcut.

Site	Forest (re. bog site)	Type[1)]	Notes
CC	Clearcut in 1994	OMT	only a few high pines left
S/79	Spruce forest (B1)	OMT	
S1	Spruce forest (B35S)	OMT	close to forest road
S2	Spruce forest (B32)	herb-rich OMT	close to dirt road
S3	Spruce forest (B35N)	OMT	
S4	Spruce forest (U/E)	MT+	
S5	Spruce forest (B20)	OMT	bordering to roadside clear-cut
S6	Spruce forest (U/W)	OMT	close to forest road

[1)] MT+ = rich *Myrtillus* type; OMT = *Oxalis-Myrtillus* type

In 1980 in Heinisuo, pitfall traps were kept between 21 May and 1 October for a total of 68 days. The plastic traps (diameter 65 mm, volume 1.7 dl, filled to about one fifth with 20% monoethylen glycole and a touch of detergent) were dug in to the ground so as to place the rind at ground level. Each trapping period lasted 6–11 days, after which the traps were emptied. One line of ten traps was placed in each of the three discrete bog habitats (sites H1–H3, Table 1). The data of the nine trapping periods were abstracted for analyses by selecting for each species in each site the highest number of traps per period where the species was found.

In 1998, we collected in the six bog and six forest sites both with pitfalls and by hand. In each site, ten pitfall traps were placed in a straight line from the bog edge in to the bog (sites U/E, U/W, B20, B32, B35S, B35N) or in to the forest (sites S1–S6), leaving 13–15 metres between successive traps. The traps were placed on 11–12 June and emptied after ten days.

Hand-collecting took place on 24–25 June within 1–2 ha around each pitfall line. To locate nests of as many as possible species present, we tried to look in all suitable microhabitats, including decaying wood, sticks, and cones of pine and spruce. A total of 65 man-hours of hand-collecting was spent on bogs, and 35 in forests. Additionally, we collected by hand in the clearcut site CC (ca. 17 man-hours on 2.7. and ca. 17 on 10 and 15 September); we also include data of hand-collecting in site S/79 (ca. 300 m^2 in ca. 5 man-hours 30 Aug. and 12 Sep. 1979, forest north of bog U/E). From each nest, ≥ 20 ants were sampled if possible, and put in a vial with 70% ethylen alcohol.

Evidently, collecting by hand was carried out differently in different periods. In 1978–79, the nests were mostly located by detailed and systematic searching of strictly limited areas. In 1998, hand-collecting covered larger areas with less detailed search. Also part of the collecting was done by experienced field myrmecologists, part by novice (but well-informed) persons, including a group of students. All the methods of collection have their pros and cons. Here, we maintain that if bogs are clearly bogs, and forests are forests, when it comes to their ant assemblages, our variation in the details of sampling only makes the comparisons more robust, but strong successional patterns from unditched bogs to forests should be revealed if present.

All ants were identified to species with the help of a Wild 5M stereomicroscope (largest magnification 50×) and keys by Collingwood (1979), Dlussky and Pisarski (1971), and Kutter (1977). We follow the nomenclature of Kutter (1977), but include *Sifolinia* (*Symbiomyrma*) to the genus *Myrmica*, according to Bolton (1995) and the phylogeny constructed from mitochondrial DNA data (R. Savolainen unpubl.). During our long-time study, *Lasius niger* was split to *L. niger* (an "urban species") and *L. platythorax* (a "rural species") (Seifert 1992). Because of region-specific practical difficulties in telling apart the two highly polycalic wood ant species, *F. aquilonia* and *F. polyctena* (Vepsäläinen & Pisarski 1981), we here treat them both under the name *F. aquilonia*. As comes to the habitats and ecological roles of the two species, they should, in the present context, be interchangeable.

3. Analyses

We analyzed the data from pitfall and hand-collecting separately, in two steps. Firstly, to find out expected regularities in successional changes of ant assemblages, we compared the sites on the basis of Morisita's similarity index for interval data (Krebs 1999: 390–391); we used the software NTSYSpc (Rohlf 1998) to calculate the indices and to cluster the sites by the UPGMA method (= unweighted pair-group method, arithmetic average; one of the SAHN = sequential, agglomerative, hierarchical, and nested clustering methods). The procedure produced similarity trees. The next step was to pinpoint the species specific for the bogs and forests, and changes in their relative frequencies as a function of the habitat. Then we used the simplified Morisita's index of niche overlap to separate species with differing habitat amplitudes from each other (Krebs 1999: 471, Rohlf 1998) — here, each study site represents a habitat patch. In the calculations, we used as the unit of observation a nest for hand-collected data, and a trap including the species in question for pitfall data.

We studied patterns of diversity changes of the assemblages as the function of habitat succession from unditched bogs through different-aged ditched bogs to forests, by estimating the Shannon–Wiener index of diversity (H', calculated with base e logs), and changing this to $e^{H'}$ = the number of equally abundant species which produces a diversity measure equitable to H'. Our choice of index is sensitive to the infrequent species in the assemblage, whereas Simpson's index would have weighted abundant species more (Krebs 1999: 444–445). To show the two aspects of heterogeneity embedded in H', we also give species diversity S (number of species) and E_{var} = Smith and Wilson's index of evenness, considered the best available index of evenness, because it is independent of species richness and sensitive to both abundant and infrequent species in the assemblage (Smith & Wilson 1996, Krebs 1999: 449–450). We calculated the indices with the software by Krebs (1998).

Because it is known that strong territorial wood ants severely impoverish the ant assemblage when present in abundance (*see* the competition hierarchy framework by Vepsäläinen & Pisarski 1982, and Savolainen *et al.* 1989), we ordered our forest patches in a sequence from lowest to highest abundance of the highly territorial wood ants. We tested the effect of wood ants in the present context by exploring correlations between the wood ants and their inferior competitors.

4. Results

4.1. Successive changes of ant assemblages

Both nest and pitfall dendrograms (though based on partially different sets of studied sites and study years) showed the same general pattern: unditched bogs and young ditchings grouped together, as did old ditchings (Figs. 1 and 2). Nest data revealed more: the 20 year-old ditching (B20) still kept to young ditchings; the same patch was studied 20 years earlier when only recently ditched (B1). The assemblage of the 32 year-old ditching (B32) had diverged far from that in the same patch 20 years earlier (B12, 12 years in 1978). One forest patch (different patches in nest *vs.* pitfall data) clustered with the old ditchings; that forest had very low (S1 in Fig. 2) or high but patchy density of wood ants (S2 in Fig. 1). The other of the 35 year-old ditchings (B35N) was already classified to a forest type instead of a bog in transitional phase (Table 2).

The structure of both dendrograms accord satisfyingly with the temporal sequence of ditching and habitat changes in this sequence. There is, however, a noteworthy difference between the two dendrograms: whereas with nest data all bogs clustered together before joining the forest cluster, with pitfall data old ditchings first joined the forest cluster, not the group of unditched bogs and younger ditching.

The forests tended to cluster according to their density of wood ants: the forest with very high density was, especially in the nest dendrogram, strikingly dissimilar within the forest cluster.

4.2. Ant species clustering

Clustering of ant species (Fig. 3) joined the three bog specialist species: *Formica uralensis, F. picea*, and *Myrmica scabrinodis*. The dendrogram was based on pitfall data from the summer of 1998, and a selected subset of species. In an alternative dendrogram (not shown here), based on an extended data set that included all the species and the three sites at Heinisuo trapped in 1980, the bog specialists still kept together, separately from the other clusters.

Two of the bog specialists were found only on unditched bogs, *F. uralensis* in two sites (a total of two pitfalls), and *F. picea* in four sites (18 pitfalls). *M. scabrinodis* was common and abundant on the bogs, but steeply declined toward older ditchings, and was completely absent from forest samples (Fig. 4). The following generalized commonness, abundance and habitat distribution characterizations are based on combined pitfall and nest data.

Of the generalists, *M. ruginodis* occurred abundantly both on bogs and in forests, but clearly predominated in forests (Fig. 4). Other species in the generalist cluster included *Lasius platythorax* and *Leptothorax acervorum*, both abundant and common species, and in the extended data *M. laevinodis* showed the same generalist pattern. The common, locally abundant *F. fusca* and *F. lemani* were found mainly on old bogs and in forests;

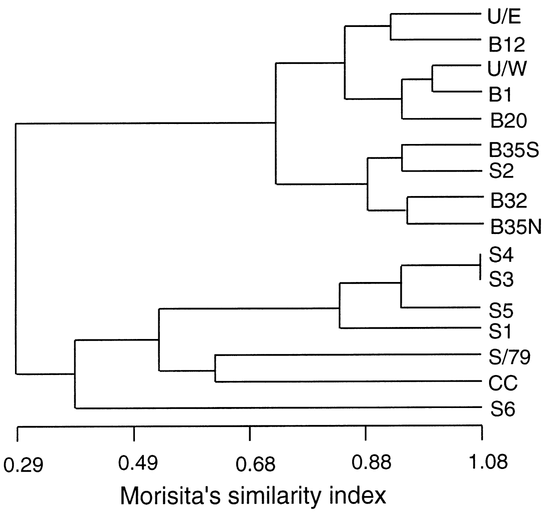

Fig. 1. Clustering of sites on the basis of nest data. Site symbols U/E and U/W = unditched bogs; B1–B35 = bogs ditched 1–35 years before sampling; CC = clearcut; S/79, S1–S6 = spruce forest (S/79, S1 = very low, S6 = very high density of wood ants).

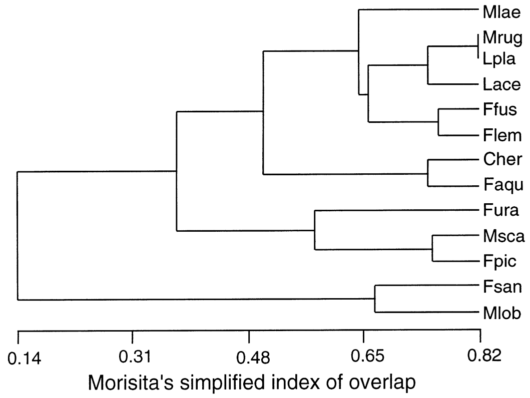

Fig. 3. Clustering of 13 ant species on the basis of site-occurrence overlaps (four species found in only one trap omitted); pitfall data of 1998 from six bog sites (given in bold in Table 1), and six forest sites (S1–S6 in Table 2). For abbreviations, *see* text.

both reached peak nest densities in the clearcut (site CC). *M. lobicornis* and *F. sanguinea* occurred commonly both on bogs and in forests, but were absent in the four and five patches with highest densities of wood ants, respectively. *F. aquilonia* reached high densities in most forest patches (but was absent in CC), and foragers found in pitfalls on bogs belonged to mounds located in the forest. The carpenter ant *Camponotus herculeanus* was found both in bogs and in forests, but never in abundance.

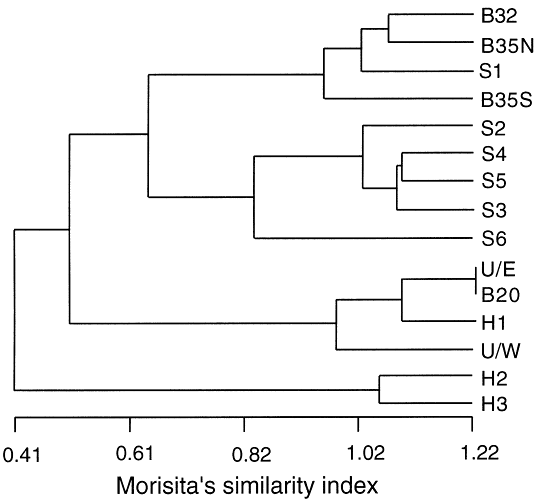

Fig. 2. Clustering of sites on the basis of pitfall data. Site symbols H1–H3 = Heinisuo bog habitats studied in 1980 (*see* Table 1); for other symbols, *see* Fig. 1.

4.3. Diversity and heterogeneity changes of ant assemblages

The number of ant species caught on bogs was fairly low, and seemed still to decrease after ditching. The species richness increased with the age of ditching, peaked within the forest clearcut, and steadily decreased with increasing wood-ant density in forests (Fig. 5). The diversity indices of local assemblages (given as the number of equally common species) followed fairly well the changes in species richness (regression model $r^2 = 0.51$, $p = 0.002$), but the evenness component showed no clear pattern.

The above result is confounded by statistically significant dependence of the number of species on the number of nests found ($r^2 = 0.34$, $p = 0.02$; 1998 data, $n = 16$ sites). Therefore, we next plotted the residuals of species richness, number of equally common species and evenness as a function of ditching age of bogs and increasing density of wood ants in forest sites; the residuals were obtained by separately regressing the three indices on the number of nests found.

Now the above pattern was amplified. The fairly low species richness of unditched bogs dived

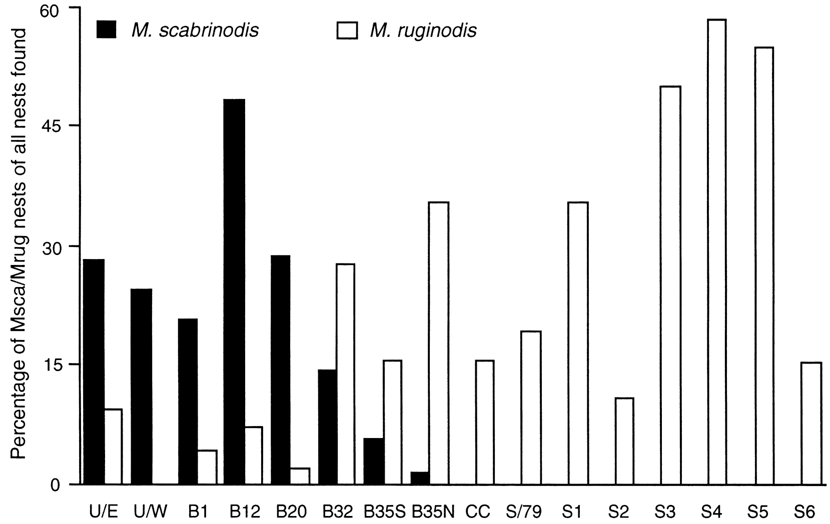

Fig. 4. The percentage of *M. scabrinodis* and *M. ruginodis* nests of all ant nests found in 16 sites, ordered from unditched bogs (U/E, U/W) through young and older ditchings (B1–B35N) and clearcut (CC) to spruce forests with increasing wood ant densities (S/79, S1–S6).

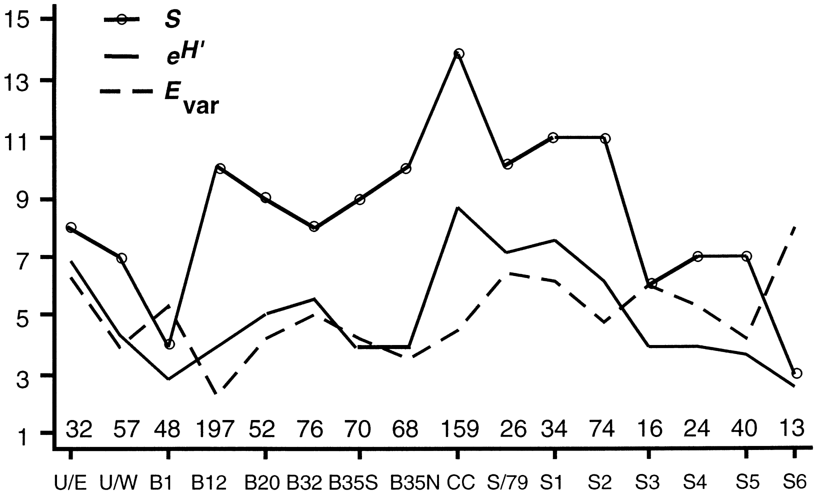

Fig. 5. Changes of diversity indices of ant assemblages in 16 sites, ordered from unditched bogs (U/E, U/W) through young and older ditchings (B1–B35N) and clearcut (CC) to spruce forests with increasing wood ant densities (S/79, S1–S6). Shannon–Wiener diversity index (*H*´) expressed as the number of equally abundant species that would produce the same diversity as *H*´(e^{H}); *S* = species richness (number of species); and E_{var} = Smith and Wilson's index of evenness. Nest data; site-specific sample sizes given above the x-axis.

to a valley of one- and 12 year-old ditchings, and returned to the unditched level at the age of two to three decades after ditching. The forest sites disturbed by high densities of wood ants had few other ant species, and the most harassed site was comparable in species poorness only to the bog site B1 one to two years after ditching. Again, the diversity pattern of local ant assemblages (the number of equally common species) followed fairly neatly that of species richness ($r^2 = 0.70$, $p = 0.000$), but the evenness component showed no regularity either relative to total diversity or species richness ($r^2 = 0.13$, $p = 0.16$ and $r^2 = 0.00$, $p = 0.92$, respectively). When site S6 with highest

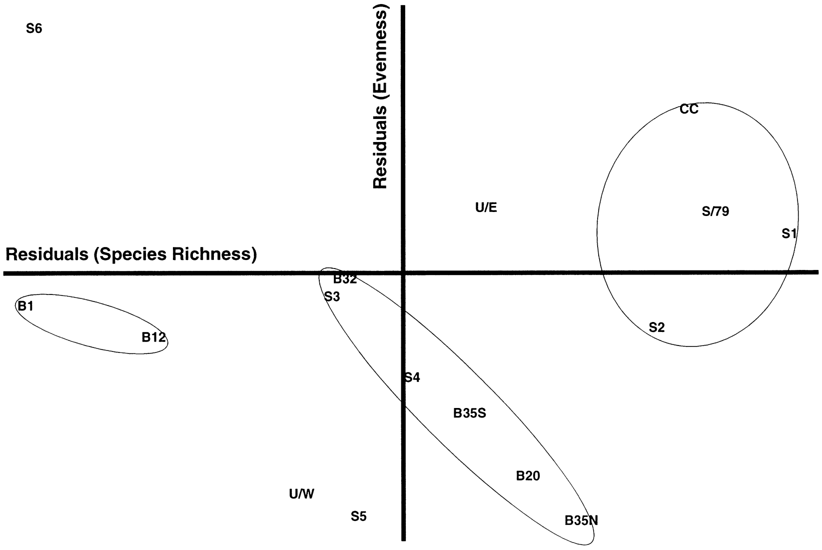

Fig. 6. The distribution of study sites (nest data) along the axes of residuals of species richness (S = number of species; min. = –3.942, max. = 3.503) and Smith and Wilson's evenness index (E_{var}; min. = –0.132, max. = 0.195); residuals obtained after regressing number of species and evenness, both separately, on the number of nests found in each site.

wood-ant density and only two other species was omitted from the regression, evenness explained 48% of the variation in the diversity index. The relative independence between the evenness and species richness components ($r^2 = 0.09$, $p = 0.28$) increased their joint explanatory power of the variation in the diversity index, i.e., the number of equally common species in the assemblages ($r^2 = 0.88$, $p = 0.000$).

However, instead of redrawing the patterns in Fig. 5 by plotting the residuals along the successional gradient, we proceeded to study species richness and evenness along separate axes, without confounding them within a single diversity index, as suggested by Mike Austin (*in litt.*, *see* Austin 1999) (Fig. 6). We still used residuals to adjust to unequal sample sizes in different loci. Now the forests without or with only weak disturbance by *Formica aquilonia* colonies, group together at the upper right space of the graph, showing high species richness and relatively even distribution of the species' nests. Forests with moderate wood-ant disturbance cluster together with older ditchings (20 years old or older), forming a gradient toward more species-rich but less even distribution of species.

Of the two unditched sites, U/W had lower species number (especially when adjusted to the larger number of nests found) and lower evenness, which was due to the high proportion (close to 50%) of *Lasius platythorax* nests, a result of a high number of suitable nest sites in decaying pine. The relatively severe wood-ant disturbance (S5) was seen in the fairly low number of other ant species present, and especially in the very uneven distribution of species present (high number of nests of litter-living, fairly wood-ant tolerant *M. ruginodis* and *M. laevinodis*). The most disturbed site (S6) had only a few nests of *M. ruginodis* and *Leptothorax acervorum* within the huge *F. aquilonia* colony, thus yielding a small number of species with the numbers of nests fairly evenly distributed. Somewhat surprisingly, young ditchings (B1, B12) had a low number of species (residuals) which were only moderately evenly distributed — this grouping was, however, much due to the unproportionately high number of nests found in B12 (n = 197, 10 spp.) and the numerical dominance of *L. platythorax* there (29% of all nests).

We interpret our results to mean that the variation of the indices follow an ecologically sound pattern along our continuum of sites, although site-specific numerical dominance of a few common and abundant species (mainly *L. platythorax* or *Myrmica* spp.) may easily affect the position of the site on the evenness axis (Fig. 6).

4.4. Effect of wood ants on the ant assemblage

The impoverishing effect of wood ants on other ants was studied with pitfall data of 1998. The 12 sites were grouped to three classes on the basis of the number of *F. aquilonia* workers in a set of ten pitfalls (Table 3); these numbers were used as estimates of the potential disturbance by wood ants on other ants, which is known to be a function of density of foraging wood ants (Savolainen & Vepsäläinen 1988, 1989).

None of the three kinds of χ^2 analyses was able to support the expected detrimental effect of wood ants on the two encounter species (Table 3). Other territorial species clearly suffered from high densities of wood ants (contribution of the high-density cell to the total χ^2 value = 55%, expected contribution 33.3%, sign negative (–); of the low-density cell, 40%, sign positive (+)). The same pattern was observed in the submissive species (cell contributions 58% (–) and 27.5% (+), respectively).

Within each wood-ant density class (i.e., rows in Table 3), a regular pattern emerged: the cell of other territorial species contributed 49%–61% (–) to the total χ^2 value (expected contribution 33.3%), whereas the cell of submissive species contributed 39%–45% (+). That is, within each wood-ant density class, the representation of other territorial species was grossly lower than expected without disturbance, and submissive species were *proportionally* overrepresented (although clearly suffering by increasing density in absolute terms, cf. the above analysis).

The two-way interaction between wood-ant density classes and competition-hierarchy categories of ants was visible in the whole-table analysis. Here, the largest contributions to the χ^2 values came from the following cells (expected cell contribution 100/9 = 11%): High-density × Territorial (29%, –), Low-density × Submissives (33%, +), and Medium-density × Submissives (21%, +); i.e., these three out of nine cells contributed most (83%) to the total χ^2 value. The bias toward an impoverishing effect on other territorial species was supported by the 7% and 6% contributions of the Territorial × Moderate/Low-density cells, respectively, whereas the four other cells contributed ≤ 2% each.

The spatial scale of the above analyses was that of one study site as covered by the set of ten pitfalls. We next shifted down to a smaller scale, and regressed the number of other ants on that of wood ants found in a pitfall. Because wood ants were scarce or absent on bogs, we included in these analyses only pitfalls in the six habitat-wise similar forest sites trapped in 1998; i.e., the total number of pitfalls in each analysis was 60 (Table 4).

Table 3. Impact of *Formica aquilonia* on other ant species. The three density categories of the wood ants are: High (1 000–4 000 workers in a set of ten pitfalls; five sets); Medium (100–400 workers; three sets); Low (0–50 workers; four sets). The table gives the number of pitfalls where the species was trapped (summed over all species in the group; the theoretical maximum is given in parentheses). Territorial species: *F. lugubris, F. pratensis, F. sanguinea, F. exsecta, F. uralensis.* Other aggressive species (encounter species by Savolainen & Vepsäläinen 1988): *Camponotus herculeanus, Lasius platythorax.* Submissive species: *Myrmica ruginodis, M. laevinodis, M. scabrinodis, M. lobicornis, Leptothorax acervorum, L. muscorum, F. fusca, F. lemani.* For the three species groups, *see* text under 5.2.3. For χ^2 tests, the expected occurrences were weighted within each column by the proportion of pitfall sets in the wood-ant density category , within each row, by the proportion of species in the competition hierarchy category of ants, and for the 3 × 3 table, by the proportion of pitfall sets (columns) and the proportion of species (rows); columns "All species" and "*M. ruginodis*" were omitted from the row and whole-table analyses. χ^2- and *p*-values for the whole table are given in bold.

Density	All species	Territorials	Encounters	Submissives	*M. ruginodis*	$\chi^2_{(2)}$ row	*p* (row)
High	39 (750)	1 (250)	5 (100)	33 (400)	26 (50)	18.24	0.0001
Medium	48 (450)	5 (150)	4 (60)	39 (240)	14 (30)	15.48	0.0004
Low	72 (600)	9 (200)	9 (80)	54 (240)	31 (40)	15.86	0.0004
$\chi^2_{(2)}$ column	19.73	8.03	2.39	12.46	3.50	**$\chi^2_{(4)}$ table**	
p (column)	0.001	0.02	0.30	0.002	0.17	**70.05**	**0.0000**

Now, the impoverishing effect of wood ants was visible in all ant species categories, although the simple linear regression models explained only a relatively small part of the total variation in the numbers of other species in the pitfalls (though, in "All species" about 40% of the variation was explained).

5. Discussion

Four main species-specific factors affect the colonization of land-upheaval islands of the Baltic Sea: (1) habitat requirements, (2) dispersal and colonization capacity, (3) dependence on other ant species, and (4) the colony's location in the local competitive hierachy among ants (Vepsäläinen & Pisarski 1982). Although the fairly deterministic process of ant assembly structuring caused by the mix of these factors is best visible during primary succession in the archipelago, the same factors are relevant in explaining the structure of ant assemblages on the mainland in primary-succession (*see* Oinonen 1956) and secondary-succession environments (Punttila *et al.* 1991). A major difference between primary and secondary succession processes is clear: whereas primary succession starts from a clean table with no ant species present, as on the small skerries in the land-upheaval area of the Baltic Sea, secondary succession practically never returns to a clean-table start. It depends much on the specifics of the major disturbance what is lost and what is left during the catastrophy. Punttila *et al.* (1994) applied the above four factors in discussing the structure of ant assemblages during forest succession following a major disturbance such as forest fire or clearcutting.

5.1. Forest disturbances and ant-assembly succession

Mature forests in the taiga region, especially spruce forests, are suitable for only a few ant species, i.e., polydomous colonies of wood ants (*F. aquilonia* and *F. polyctena*), the carpenter ant *Camponotus herculeanus*, and *Myrmica ruginodis*. Other northern ant species need or prefer more open, drier and warmer habitats. Clearcutting creates suitable habitat for the latter group of ants while causing local extinction of wood ants (Punttila *et al.* 1994). Such death of the local *F. aquilonia* population probably took place in the clearcut CC of our study. Before clearcutting, the site had been optimal habitat for the species, now absent from there.

Extinctions are partially due to severe decrease in tree-living aphid populations, the main food resource of wood ants (Vepsäläinen & Wuorenrinne 1978). Secondly, maintenance of route fidelity and orientation of wood ants to the possibly remaining aphid trees is hampered by loss of necessary visual orientation cues, especially after winter-time clearcutting (Rosengren & Pamilo 1978). Because wood ants, when present, are key species in organizing the whole ant community and affect also many other ground-living arthropods (Vepsäläinen & Pisarski 1982, Savolainen & Vepsäläinen 1988, Punttila *et al.* 1996), their local extinction will affect drastically the assembly process during secondary succession.

Decreased competitive pressure by wood ants facilitates colonization of the open habitat created by clearcutting by other species. Although colonization of islands by *Formica* species of the *fusca* group, capable of independent colony foundation, is severely constrained by open water (Vepsä-

Table 4. Correlation between the numbers of wood ants and those of other ant species caught in pitfalls (bog pitfall sets only, d.f. = 58). For the competition hierarchy categories of ants, *see* Table 3. Pearson's correlation coefficients (*r*), *p*-values and r^2 are given.

	All species	Territorials	Encounters	Submissives	*M. ruginodis*
r	–0.64	–0.46	–0.37	–0.51	–0.51
p	0.000	0.000	0.003	0.000	0.000
r^2	0.41	0.21	0.14	0.26	0.26

läinen & Pisarski 1982), their dispersal and colonization of clearcuts is easy in a mosaic of forest and more open habitat; consequently, their colonies are abundant in early stages of forest succession (Punttila *et al.* 1991). *Fusca*-group species are needed by the facultative slave-maker *F. sanguinea* during colony foundation, and they also serve as potential slave sources later on during the colony cycle. This explains why *F. sanguinea*, an efficient disperser and good colonizer (Oinonen 1956, Punttila *et al.* 1991) is able to colonize rapidly new clearcuts (Punttila *et al.* 1994).

All European mound-building *Formica* species are known or assumed to establish their colonies in new areas through temporary parasitism in the nests of the *fusca* group (Gößwald 1989), but their colonization success varies greatly among the species. Generally, queens of monogynous, monodomous species are thought to be more efficient temporary social parasites than are queens of polygynous, polydomous species (Gößwald 1951). Our present results of the species composition of the clearcut (CC) agree with earlier findings. Of the mound-building species found in CC, *F. truncorum*, *F. sanguinea*, *F. exsecta* and *F. pressilabris* spread both by flight dispersal followed by temporary parasitism ("monogynous tactic"), and locally by colony splitting ("polygynous tactic") (*see* Sundström 1993, Pamilo 1981, Pisarski 1982, Czechowski 1975, respectively for the four species), whereas Finnish *F. rufa* and *F. lugubris* usually follow the monogynous tactic (Vepsäläinen & Wuorenrinne 1978, Rosengren *et al.* 1979). As expected, the highly polygynous and polydomous *F. aquilonia* had not yet (re)colonized CC.

The high density of nests of the above potentially polydomous, mound-building *Formica* species in the clearcut CC, together with their potential slave species *F. fusca* and *F. lemani* during colony foundation, and the high density of *M. ruginodis* known to be an effective local disperser by colony splitting, all agree with the results obtained by Punttila *et al.* (1996), Punttila (1996), and Punttila and Haila (1996) in early successional environments of clearcut, fragmented and burnt southern Finnish boreal forests, respectively.

After smaller-scale tree felling, the competitive impact of wood ants on other species may still weaken, but highly polygynic and polydomous *F. aquilonia* and *F. polyctena* may avoid complete local extinction by nest splitting (Vepsäläinen & Wuorenrinne 1978). Consequently, wood ants would then figure as important key species already during the early phases of the secondary succession. This is often true also after forest fires, which often leave practically untouched pockets of forest from where surviving colonies of wood ants can spread by splitting to recovering burnt areas (Punttila *et al.* 1994).

5.2. Successional changes of bog assemblages after ditching

5.2.1. Impact on bog specialists

In the following, we will concentrate on successional changes along the continuum from virgin bogs through different-aged ditched bogs to forest. Draining differs from the above-discussed major habitat disturbances in a crucial aspect: it does not change the habitat back to an earlier successional stage of the site as forests fires and clearcutting do, and the succession does not start from a site totally void of species as in primary-succession loci. Peatlands are old formations, in our area the age of ombrotrophic bogs is measured in thousands of years (Tolonen 1987), and they are not following a natural process toward a final forest stage. However, the goal of foresters is to change bogs to forests by ditching. We therefore first discuss the impact of ditching on bog specialists.

In our study, we localized three bog specialists: *Formica uralensis*, *F. picea* and *Myrmica scabrinodis*. Although the two *Formica* species are eurytopic within their extensive distribution area east of the Ural Mountains, they are true bog species in northern Europe (Dlusskij 1967). In our study they were found only on virgin bogs, and draining of bogs means inevident local extinction for the species. Because of the large scale and high incidence of ditching of bogs in northern Europe (*see* Introduction), such local extinctions are liable to sum up to severe thinning of populations and increased extinction risk on a large, geographical and national scale.

M. scabrinodis is known to live in a very wide range of habitats (Collingwood 1979), but in Finland, especially within the extensive taiga region, it lives predominantly on bogs, where it may reach very high nest densities (Saaristo 1995). An obligate social parasite of other *Myrmica* species, *M. karavajevi* (Collingwood 1979), has been found in Finland only in bog nests of *M. scabrinodis*. Saaristo (1995) suggested that quite possibly the parasite can be found in Finland on any bog with a sufficiently strong population of *M. scabrinodis*. Indeed, our year 1998 traps were operated through the season, and on 13 August a female *M. karavajevi* was found in a pitfall jar in U/W, and next summer we located there a *scabrinodis* nest with plenty of sexual offspring of *karavajevi*. Again, large-scale draining of bogs would mean a deathblow to the potentially healthy but poorly documented Finnish population of the globally rare *M. karavajevi.*

5.2.2. The fate of generalists after ditching

During early succession of forest sites after a major disturbance, many common and abundant generalist species (*see* Fig. 3 and the accompanying text) have improved chances to colonize the site, because of both improved habitat quality and usually weakened competition (above). Successional changes of the generalist ant fauna after ditching is different, because the species already live on virgin bogs.

In our study, the mature forests used in comparison with bogs of different successional stages were (because of regional conditions) spruce forests. A more natural set of forest types would have been those growing mainly pine, because those are the forests toward which pine-growing bogs are expected to converge after draining. Our experience from studies in pine-dominated, dry and open forests (K. Vepsäläinen & B. Pisarski unpubl., K. Vepsäläinen & R. Savolainen unpubl.) and in spruce-dominated forests (Savolainen *et al.* 1989) let us safely expect that no generalist ant species is lost because of successional habitat changes following ditching. This conclusion is supported by our present results. Without doubt the actual and relative abundances of species may change along the succession. This is clearly visible in our *M. ruginodis* data, where this generalist species has a clear bias for mature spruce forests — a result which is in harmony with the results of Punttila *et al.* (1994).

Although habitat attributes have an important effect on the structure and structuring of ant assemblages, their effect is grossly confused by the overwhelming importance of competition among ants, especially between wood ants and other ant species. In the following, we discuss this aspect in the context of the competitive hierarchy among ants (Vepsäläinen & Pisarski 1982, Savolainen & Vepsäläinen 1988).

5.2.3. The role of competition in ant assembly process

Vepsäläinen and Pisarski (1982) classified the Finnish ant species to a three-tiered hierarchy from general winners at the top to general losers at the bottom. Top dominants are *territorial*, whereas intermediate-level *encounter* species are not, but tend to defend concentrated food sources. It follows that locally highest-level territorials will exclude other territorials and species of the intermediate level. Lowest-level species are *submissive* and avoid conflicts by escaping, which may allow them coexistence with higher-level species (Vepsäläinen & Pisarski 1982, Pisarski & Vepsäläinen 1989, Hölldobler & Wilson 1990).

Our results from mature spruce forest sites show the strong impoverishing effect of the highly polydomous *F. aquilonia* on the local ant assemblage (Tables 3 and 4), even though our analyses suffered from unequal power of the statisitical tests — a result of grossly uneven sample sizes. In the extreme high-density wood of wood-ant foragers, only a few nests of two other species, *M. ruginodis* and *Leptothorax acervorum*, were found. Both are Myrmicine species able to forage in the litter and avoid most of the disturbance by wood ants, although their nests are doomed to be destroyed when found by wood ants (Savolainen & Vepsäläinen 1988, 1989). However, large small-scale variation in wood-ant forager densities within their territory renders submissive species with evasive foragers (e.g., *fusca*-group species, *Myrmica* spp., *Leptothorax* spp.) microsites where they may nest and produce sexual offspring, though probably with lower success than outside the territory (Savolainen & Vepsäläinen 1989; for details *see* Pisarski & Vepsäläinen 1989, Vepsäläinen & Savolainen 1990, Savolainen 1990, 1991). Similar keystone roles of top dominants have been described in widely different biomes from the taiga to wet and dry tropics on several continents (Dlusskij 1981, Savolainen & Vepsäläinen 1988, Savolainen *et al.* 1989, Hölldobler & Wilson 1990, Punttila *et al.* 1996, Andersen 1997a); however, the specifics of behavioural dominance are everywhere crucially scale-dependent (Andersen 1997b).

One might expect that in a mosaic of forests, and virgin and different-aged ditched bogs, *F. aquilonia* would easily spread by colony splitting over all habitat types. There are reasons, however, why this need not be the case, as found in our present study. Virgin bogs and early-succession ditched bogs seem to be microclimatically unsuitable to wood ants which are true species of the taiga biome. Bogs are periodically hot sites, which intervenes with the foraging activity of wood ants with lower optimal temperature regimes. Overwintering may also be problematic on bogs, because wood ants typically spend the winter deep down in the nest cells or in the ground (Gößwald 1989). It is also possible that trees with suitable aphid species for the wood ants are too scarce on bogs to maintain their individual-rich colonies — between-year variation in aphid trees may affect the foraging pattern of wood ants even in suitable habitats (Vepsäläinen & Savolainen 1994). On the contrary, *F. sanguinea* is able to tolerate high temperatures and seasonal vicissitudes on bogs, and in suitable sites build up strong polydomous societies. This is also true in the taiga clearcuts (Punttila *et al.* 1996) and in hot southern Finnish sand dune areas (Gallé 1991).

After ditching of bogs, pre-emption of the sites by *F. sanguinea* may slow down colonization by wood ants by the means of queen predation and competition (Rosengren *et al.* 1979), and by reducing the densities of *fusca*-group nests (Oinonen 1956, Punttila *et al.* 1996). In the present study, *F. aquilonia* mounds were found in low densities only on ditched bogs of the age of 20 years or older. On the 32 year-old bog, one *F. sanguinea* colony had small *F. aquilonia* workers as their slaves — another sign of the slavemaker's potential to interfere with the colonization of wood ants, because slave raids tend to extinguish the raided colonies (*see* Punttila *et al.* 1991 re. *fusca*-group species, the usual slave species). Indeed, Punttila and Haila (1996) suggested that *F. sanguinea* is one of the keystone species in open successional forest of the taiga, and this may be locally true on virgin bogs and young ditchings as well. But earlier experience (Vepsäläinen & Pisarski 1982) has taught that, given time and suitable habitat, *F. aquilonia* or *F. polyctena* will unavoidably spread by colony splitting and gradually outcompete by overwhelming workforce other territorial species, i.e., the above mound-building species. For many territorial species (e.g., *F. truncorum*, *F. sanguinea*, *F. exsecta* and *F. pressilabris*) the gradual closening of the forest canopy will work to the same end, local extinction (Punttila 1996).

A final important aspect in ant assembly processes is the role of chance. Vepsäläinen and Pisarski (1982) suggested, while discussing colonization of land-upheaval islands, that the island-specific establishment of the three common and abundant *Myrmica* species, *M. ruginodis*, *M. laevinodis* and *M. scabrinodis*, may be explained by priority effect. Chance may play the most significant role in dispersal to and colonization of an island large enough to provide first suitable habitat patches for the species, and pre-emption by the first-comer would keep the other two species out until plenty of suitable habitat is available for *Myrmica*. Our present findings on the bogs indicated patchy high nest-density strongholds of a single *Myrmica* species, with one of the three species vicariating in turn.

The details of ant assembly processes are still complicated by indirect competitive effects among the species, as shown already by Oinonen (1956) and Punttila *et al.* (1996). For example, the scarcity of *Lasius platythorax* in the clearcut CC with plenty of suitable nest sites to the species, is best explained by competition with stronger, territorial *Formica* species (abundant on the site) (Savolainen & Vepsäläinen 1988), and that would favour the locally abundant submissive *Myrmica* and *fusca*-group species, as suggested by Punttila *et al.* (1996).

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