

# Ant communities in fragments of old-growth taiga and managed surroundings

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The structure of ant communities was studied by sampling with pitfall traps in 24 mixed coniferous old-growth fragments (>140 yrs old), their edges, and managed surroundings of different ages in southern Finland. The old-forest ant community consisted of only three common shade-tolerant species, *Formica aquilonia*, *Myrmica ruginodis* and *Camponotus herculeanus*, whereas most of the ant species inhabited the early stages of forest succession. The size of the fragment affected only slightly the ant community. The most common territorial wood ant, *F. aquilonia*, structured the ant community by suppressing other species, although not equally so. The ant-community structure in the context of forest succession and landscape structure is discussed, and the successions in managed forests compared to those occurring after more natural disturbances. Forestry has changed the dynamics of succession and structural characteristics of the forest stands. Important changes of the landscape affecting forest-ant species are age-distribution of the forests and the fragmentation of old-growth forests accompanied by an increased proportion of edge habitats: open-country species have gained a greater inhabitable area and the relative abundances of the territorial wood-ant species (*Formica* s. str.) have changed. The multinest supercolonies of *F. aquilonia* have decreased, whereas species such as *F. lugubris*, which in our study area tend to be monodomous, have benefitted.

## 1. Introduction

A crucial question in maintaining biotic diversity in managed boreal forests is how their spatial heterogeneity and disturbance regimes differ from those that prevailed before modern forestry (Esseen et al. 1992, Haila et al. 1994). With such

knowledge we might be able to identify the most important characteristics for the functioning of this forest ecosystem and further, to incorporate such features into forest management (Harris 1984, Franklin 1988, Harris & Eisenberg 1989, Brussard 1991, Liljelund et al. 1992). One way to obtain such knowledge is to compare faunas

of naturally regenerating forests to those of managed forests. This, however, is rarely possible in north-western Europe because in most areas natural succession does not exist anymore. To overcome this problem, comparisons have been made between late-successional stages of managed forests and naturally regenerated old-growth forests in nature reserves (for invertebrates, see Huhta 1965, 1971, 1976, Huhta et al. 1967, 1969, Huhta & Koskenniemi 1975, Biström & Väisänen 1988, Niemelä et al. 1988, Pajunen 1988, Väisänen et al. 1993).

Compared to naturally regenerating forests, succession in managed forests includes accelerated successional cycles and decreased vegetational heterogeneity (Esseen et al. 1992). In addition, fragmentation has significantly reduced the size of old-growth patches and their total area. Consequently, the proportion of edge habitats in forest landscapes has increased (Merriam & Wegner 1992, Halme & Niemelä 1993, and references therein). An urgent task is to explore how these changes in the forest ecosystems have affected forest-dwelling organisms.

The multinest colonies of some wood-ant species (*Formica* s. str.) may be comparable in age to trees (Oinonen 1956, 1958). These ant species affect the distribution and abundance of other ants (Vepsäläinen & Pisarski 1982, Savolainen & Vepsäläinen 1988, 1989, Savolainen et al. 1989) and many other species of ground-living arthropods (Kaczmarek 1963, Kolbe 1968, 1969, Cherix & Bourne 1980, Niemelä et al. 1992), and canopy-dwelling invertebrates (Laine & Niemelä 1980, Skinner & Whittaker 1981, Fowler & MacGarvin 1985, Warrington & Whittaker 1985a, 1985b; see also the reviews by Gösswald 1951a, Adlung 1966, Way & Khoo 1992), as well as a large variety of myrmecophilous invertebrates (Larsson 1943, Lehtinen 1987, Gösswald 1989, Hölldobler & Wilson 1990). They also are an important food resource (Gösswald 1990, Elgmork & Kaasa 1992) and possibly even competitors of some vertebrates (Haemig 1992, Aho et al. 1993). A great number of forest plants are dispersed by ants (Buckley 1982a, 1982b, Hölldobler & Wilson 1990); ants may affect the growth of trees (Whittaker & Warrington 1985, Rosengren & Sundström 1991, Whittaker 1991, Mahdi & Whittaker 1993); food-

transportation by ant workers is of great importance in the nutrient cycles (Oinonen 1956, Petal 1978); and in the long run, their nest-digging activities affect forest soils (Oinonen 1956, Petal 1978). Therefore, the ecological effects of ants extend over most trophic levels, making them an integral part of the taiga ecosystems and, consequently, essential study objects in the context of forest ecology.

However, quantitative data on the relation of ant-community succession to forest succession (Oinonen 1956, Gallé 1991, Punttila et al. 1991, Punttila, Haila, Tukia, unpubl.) as well as on the ant-community structure in old-growth forests (Savolainen et al. 1989, Punttila et al. 1991) in the western palearctic taiga are scarce. In this paper we provide some baseline data on the distribution of ants in coniferous forests in southern Finland and explore the effects of the territorial wood ants on the overall structure of ant communities. We focus on three aspects of the effects of forestry on ant communities: (1) How are the ant species distributed along the successional gradient in managed forests? (2) Does the size of old-forest fragments affect ant-community structure? (3) Do the ant communities of fragment edges differ from those of fragment interiors? We relate these aspects to the autecology of the species, to species interactions, and to the disturbance cycles during more primeval conditions and then discuss forestry-driven changes in the present ant communities of the taiga.

## 2. Material and methods

### 2.1. Study area and sampling procedure

We conducted our study in southern Finland (62°N, 24°E): within and close to Seitsemien National Park, in the surroundings of Hyttälä Forest Research Station, and in Helvetinjärvi National Park (for a more detailed description of the study area, see Niemelä et al. 1988). The study areas are situated within an area of ca. 2500 km<sup>2</sup> on the border between southern and mid-boreal taiga zones.

The ants were collected in 72 sampling sites, 24 sites each in the interiors of old-growth forests, their edges and surroundings. Most of the

old-growth fragments (0.4–101 ha, mostly more than 140 yrs old) were in nearly primeval condition. They were mesic, dominated by Norway spruce (*Picea abies*) and/or Scots pine (*Pinus sylvestris*) with an admixture of birches (*Betula* spp.) and aspen (*Populus tremula*). The surroundings comprised mostly managed forests of various forest-site types, with their age varying from under 20 years to under 140 years. To relate the distribution of invertebrates to the environment, several habitat characteristics were measured (for details, see Niemelä et al. 1988).

The forest-floor arthropods were sampled with pitfall traps (for the method, see Niemelä et al. 1988; for the suitability of the method for ants, see Punttila et al. 1991, Punttila, Haila, Tukia, unpubl., and references therein) which were in operation for five days between 19 to 26 August 1984. At each sampling site, a set of 15 traps was placed in a regular  $3 \times 5$  grid at ca. 3–4 m distance apart, covering an area of ca. 0.01 ha. The ant catches of the 15 traps in each set were combined. Despite the short trapping period, we regard these data as representative for the purposes of this study, because in our study area, ant species do not show seasonal segregation (Punttila et al. 1991 and unpublished). Further, five-day pitfall-trapping periods gave rather similar results for species composition of an old-forest ant community as did combined samples from several five-day trapping periods (Punttila et al., unpublished). The ants were identified by PP using the keys of Dlusskij & Pisarski (1971), Collingwood (1979) and Douwes (1981). The nomenclature follows Collingwood (1979).

## 2.2. Statistical analyses

We used redundancy analysis (RDA; CANOCO statistical software, Ter Braak 1987) to relate the variation in ant catches to environmental characteristics measured at the sampling sites. In this analysis, we used eight environmental variables (see Fig. 2). Two of these summarized the major gradients in floristic variation (the scores of the two first axes of a detrended correspondence analysis (DCA; CANOCO statistical software, Ter Braak 1987) of the vegetation of the sampling sites;  $\ln(x+1)$ -transformation and downweighting

of rare species applied). For the ant data in the redundancy analysis, we used  $\log_{10}(x+1)$ -transformation. In this analysis, we included only species occurring in >5% of the sampling sites: 11 ant species in total. We excluded three samples from the fragment surroundings for this analysis: one of them was clearcut before the vegetation descriptions were done, one was an open bog, and the field-layer vegetation of one site was of an entirely different type from that of the others. The bog site was excluded from all of the following analyses.

In exploring environmental contingencies in the co-occurrence of other ant species with the dominating wood ant *F. aquilonia*, we used three-way contingency tables (BMDP4F statistical software; Dixon 1990). We divided the ant data into contingency classes using medians as guidelines. In interpreting the log-linear models obtained, we followed Toft (1984; see also Savolainen & Vepsäläinen 1988, Vepsäläinen et al. 1988). In all analyses of the ant data, we used non-parametric statistics because our data were not normally distributed (tested with BMDP2D; Dixon 1990). We used Kruskal-Wallis one-way ANOVA and pairwise Tukey-type *a-posteriori* tests or Mann-Whitney *U*-tests, and Spearman rank correlation (BMDP3S; Dixon 1990) when analysing the distribution of ant species, employing these tests only when the species occurred in at least 2/3 of the sites concerned in the analysis. In addition, we applied log-likelihood-ratio tests ( $G^2$ ; BMDP4F; Dixon 1990) or Fisher's exact tests for two-by-two/three tables (StatXact statistical software 1991) to test the equality of occurrences of the ants in low and high numbers (defined by the medians) in the samples.

## 3. Results

The ant data comprised 19 species; 144048 workers of 17 species and 94 queens of 11 species (Appendix 1). In the worker data, the five most abundant species included three species of wood ants (*Formica aquilonia*, *F. rufa*, *F. lugubris*), and *Myrmica ruginodis* and *Camponotus herculeanus*. Species with the widest distribution among our sampling sites were *M. ruginodis* (caught in 60 of the 71 sites), *F. aquilonia* (49), *C.*

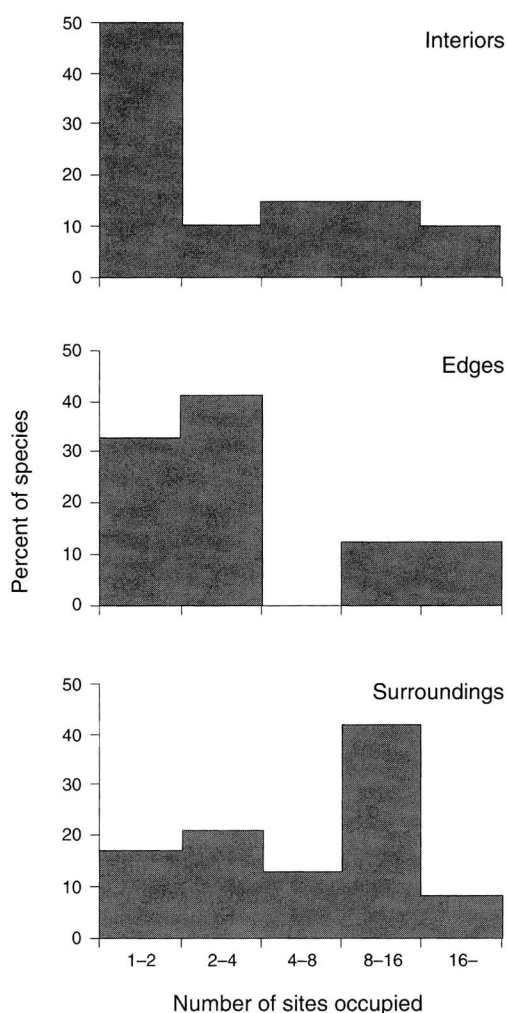


Fig. 1. Species-incidence distributions in the fragment interiors, edges and surroundings, bars indicating the proportion (%) of species in each incidence class (i.e., number of sites occupied by a given species). Border-incidence species are divided between the neighbouring classes.

*herculeanus* (30), *F. lugubris* (15) and *F. lemani* (14). In the old-growth fragments and their edges more than half of the species occurred in only 1–4 sites, whereas in the surrounding younger forests most species occurred in at least four sites (Fig. 1). The same species, *F. aquilonia*, *M. ruginodis* and *C. herculeanus*, were the most common ones in fragment interiors, edges and surroundings. This similarity in species compo-

sition resulted from the shadiness of the surrounding forests: only seven of these forests were younger than 40 years. Thus, in most of the following analyses we focus on the total number of species and on the occurrences of the common species mentioned above.

### 3.1. The forest environment and the ant community

In the RDA ordination, the ant communities formed a continuum from the fragment interiors through the edges to the younger and more open surroundings (Fig. 2A). This gradient was roughly parallel to the gradients in tree-canopy cover, basal area, forest height and floristic composition (DCA-axis 2). As the DCA-axes of the vegetation of the sampling sites did not run along the environmental gradients in the DCA-ordination, no clear interpretation can be given to DCA-axis 1, whereas DCA-axis 2 related approximately to the openness gradient of the sampling sites. In addition to the age of the forest, the presence of the most common wood-ant, *F. aquilonia*, affected the ant communities as a whole (Fig. 2B).

The sampling sites formed two distinct clusters, depending on the abundance (high numbers vs practical absence) of this territorial species in the RDA ordination (the scores of this species were clearly separated from scores of the others; see Fig. 2B). We were unable to find any environmental gradient to account for this pattern: in the plant data, there was no such detectable segregation but a weak continuum from open to closed sites. Thus, the ordination of the samples reflected competitive suppression of the other species by *F. aquilonia* on the one hand, and the effect of forest age on the other.

### 3.2. Effects of forest age

The median number of ant species was highest in the younger age classes (Table 1), with a significant difference between the youngest and the oldest sites (*a-posteriori* tests). The result was similar when we compared the number of sites with low vs high numbers of species in the age classes. The medians of *M. ruginodis* differed

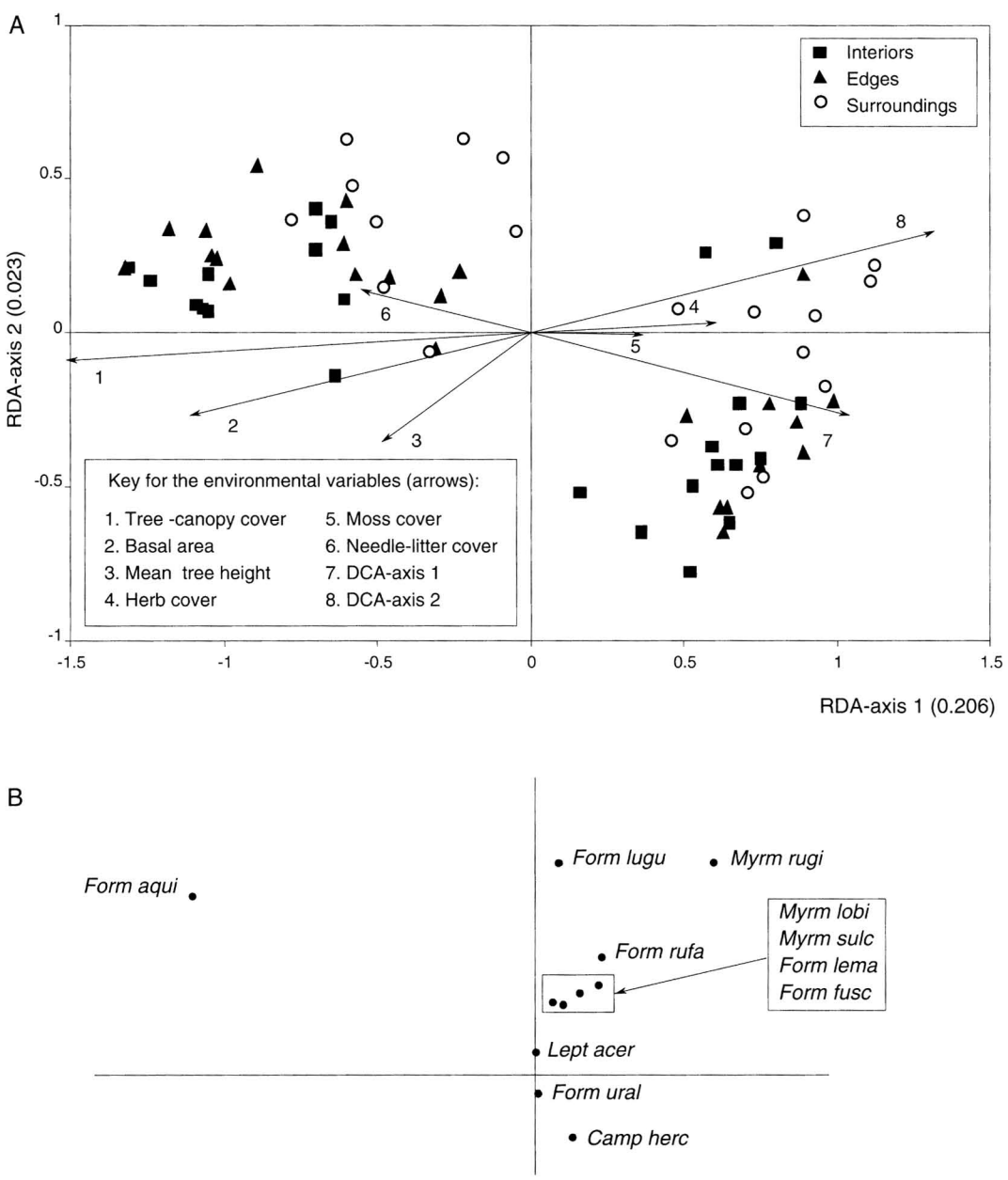


Fig. 2. — A. RDA ordination of sampling sites according to their ant samples. Keys for environmental variables and sampling-site locations given in the figure. Eigenvalues of the RDA axes given in parentheses. — B. RDA ordination of ant species in sampling sites (parallel to 2A).

among the age classes, being highest in the 41 to 80-year old sites, which differed from the oldest but not from the youngest ones. *M. ruginodis* also occurred in high numbers more often than expected in the younger sites. The medians of *F.*

*aquilonia* did not differ among the age classes. Both *F. aquilonia* and *C. herculeanus* occurred in low and high numbers independent of forest age. For *F. aquilonia*, however, the result may have been biased because of the long foraging ranges

of the workers — especially in a forest landscape where small forest stands of different age are distributed in a mosaic-like manner, catches of the wood-ant workers indicate distribution of foraging activity primarily and not the locations of the mounds (see Punttila et al. 1991). The numbers and diversity of queen ants were highest in the younger fragment surroundings (Appendix 1).

3.3. Effects of fragment size and edge

The median number of ant species caught tended to be slightly lower in the larger fragments (>20 ha) than in the smaller ones (<21 ha), but not significantly so (Table 2). Furthermore, the negative correlation between fragment size and number of ant species was nonsignificant. However, in the smaller fragments the number of sites with high numbers of species was higher than expected. The medians of *F. aquilonia* did not differ between the two fragment-size classes, and the correlation between the fragment size

and the numbers of *F. aquilonia* was nonsignificant. Further, *M. ruginodis*, *C. herculeanus* and *F. aquilonia* occurred in low and high numbers independently of the fragment size.

The median number of species was higher in the edges than in the fragment interiors (Table 3). Neither the medians of *M. ruginodis* nor *F. aquilonia* differed between the edges and the fragment interiors. Further, *M. ruginodis*, *C. herculeanus* and *F. aquilonia* occurred in low and high numbers independently of the sampling-site location.

3.4. Species interactions and habitat effects

The occurrences of other species correlated negatively with the abundance of *F. aquilonia* (Fig. 3, Table 4). In order to explore habitat effects on the co-occurrence of other species with *F. aquilonia*, we used log-linear models. The forest age formed the clearest environmental gradient in the ant data according to the redundancy analysis, and thus we divided the sampling sites into contingency classes

Table 1. Quartiles (Q<sub>1</sub>, Median, Q<sub>3</sub>) of numbers of species and abundances of *M. ruginodis*, *C. herculeanus* and *F. aquilonia* in forest age-classes (<41, 41–80, and >81 yrs; numbers of sampling sites in classes are 7, 7, and 33, respectively). Differences among the medians were tested with Kruskal-Wallis one-way ANOVA (*H*, *df* = 2). In the lower half of the table are numbers of sampling sites with low and high numbers (defined by medians) of species (Median = 3), *M. ruginodis* (M = 8), *C. herculeanus* (M = 0) and *F. aquilonia* (M = 7) in the age classes. Equality of occurrences in low and high numbers were tested with Fisher's exact test. (– = not tested because of scanty occurrences.)

Age class:		<41 yrs			41–80 yrs			>80 yrs			<i>H</i>	<i>P</i>
		Q <sub>1</sub>	M	Q <sub>3</sub>	Q <sub>1</sub>	M	Q <sub>3</sub>	Q <sub>1</sub>	M	Q <sub>3</sub>		
Species												
Number of spp.		4	6	6	3	4	5	1.5	2	4	13.95	0.001
<i>M. ruginodis</i>		9	15	30	19	47	56	0	4	12	10.75	0.005
<i>C. herculeanus</i>		0	0	1	0	1	2	0	0	2.5	–	
<i>F. aquilonia</i>		0	202	712	0	2	1090	0	3	2564.5	0.24	0.886
Sites												
Number of spp.	low	1			3			24				0.012
	high	6			4			9				
<i>M. ruginodis</i>	low	1			1			21				0.010
	high	6			6			12				
<i>C. herculeanus</i>	low	5			3			19				0.555
	high	2			4			14				
<i>F. aquilonia</i>	low	2			4			18				0.435
	high	5			3			15				

Table 2. Quartiles (Q<sub>1</sub>, Median, Q<sub>3</sub>) of numbers of species and abundances of *M. ruginodis*, *C. herculeanus* and *F. aquilonia* in old-forest fragment size classes (<21 and >20 ha; *n* = 12 in both classes). Differences between medians were tested with Mann-Whitney rank-sum test (*U*; *df* = 1). Also Spearman rank correlations (*r<sub>s</sub>*; *N* = 24) between fragment size and number of species, and abundance of *F. aquilonia* are given. In the lower half of the table, we give numbers of sampling sites with low and high numbers (defined by medians) of species (Median = 2), *M. ruginodis* (*M* = 4), *C. herculeanus* (*M* = 0) and *F. aquilonia* (*M* = 5) in fragment-size classes. Equality of occurrences in low and high numbers were tested with Fisher's exact test. (– = not tested because of scanty occurrences.)

Size class:		<21 ha			>20 ha			U	P	r <sub>s</sub>	P
		Q <sub>1</sub>	M	Q <sub>3</sub>	Q <sub>1</sub>	M	Q <sub>3</sub>				
Species											
Number of spp.		1.25	3	3.75	1	2	2	101.0	0.081	−0.338	>0.1
M. ruginodis		0	6.5	11.5	0	2	11.75	–		–	
C. herculeanus		0	0	2.75	0	0	3.75	–		–	
F. aquilonia		1	2	1549.5	0	1522	5527.75	56.0	0.351	−0.048	>0.1
Sites											
Number of spp.		low	5			11					
		high	7			1					0.027
M. ruginodis		low	6			8					
		high	6			4					0.680
C. herculeanus		low	7			9					
		high	5			3					0.667
F. aquilonia		low	7			5					
		high	5			7					0.684

Table 3. Quartiles (Q<sub>1</sub>, Median, Q<sub>3</sub>) of numbers of species and abundances of *M. ruginodis*, *C. herculeanus* and *F. aquilonia* in fragment interiors and edges (*n* = 24 in both classes). Differences between medians were tested with Mann-Whitney rank-sum test (*U*; *df* = 1). In the lower half of table, we give numbers of sampling sites with low and high numbers (defined by medians) of species (Median = 2), *M. ruginodis* (*M* = 4), *C. herculeanus* (*M* = 0) and *F. aquilonia* (*M* = 251) in fragment interiors and edges. Equality of occurrences in low and high numbers were tested with log-likelihood-ratio test (*G<sup>2</sup>*; *df* = 1). (– = not tested because of scanty occurrences.)

Sampling-site location:		Interiors			Edges			<i>U</i>	<i>G</i> <sup>2</sup>	<i>P</i>
		Q <sub>1</sub>	M	Q <sub>3</sub>	Q <sub>1</sub>	M	Q <sub>3</sub>			
Species										
Number of spp.		1	2	3	2	3	3	183.0		0.024
<i>M. ruginodis</i>		0	4	11.5	2	8.5	25.75	196.5		0.058
<i>C. herculeanus</i>		0	0	2.75	0	0	5	—		
<i>F. aquilonia</i>		0.25	5	3628	0	336.5	3799.5	280.5		0.876
Sites										
Number of spp.	low		16			7				
	high		8			17			6.93	0.009
<i>M. ruginodis</i>	low		14			10				
	high		10			14			1.34	0.247
<i>C. herculeanus</i>	low		16			14				
	high		8			10			0.36	0.551
<i>F. aquilonia</i>	low		13			11				
	high		11			13			0.33	0.564



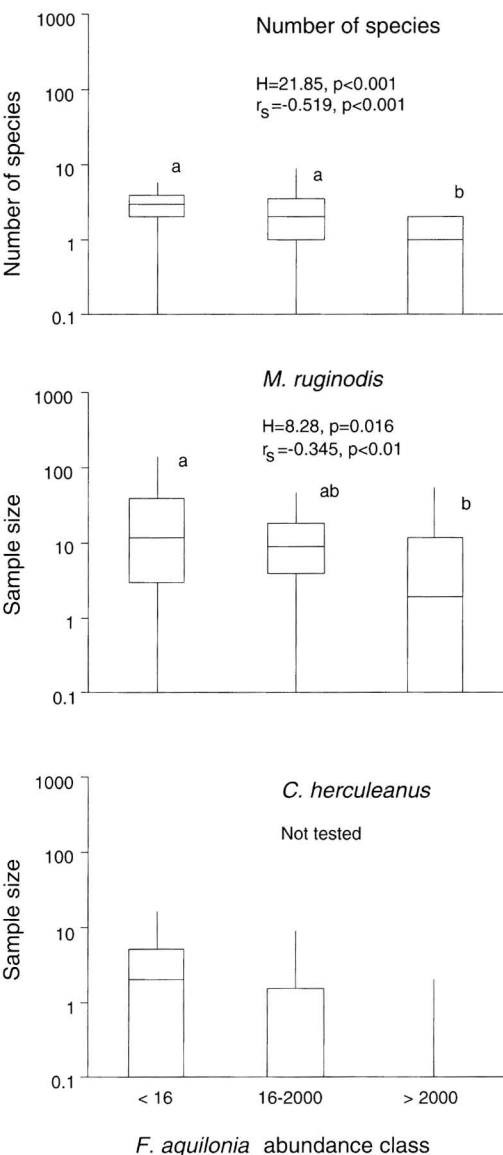


Fig. 3. Numbers of other species and abundances (quartiles, min. and max.) of *M. ruginodis* and *C. herculeanus* in sampling sites divided into three classes according to abundance of *F. aquilonia* in samples (<16 workers in the sample,  $n = 35$  sites; 16–2000,  $n = 17$ ; and >2000,  $n = 19$ ). Differences among medians tested with Kruskal-Wallis one-way ANOVA ( $H$ ,  $df = 2$ ). Letter code indicates the location of significant differences according to *a-posteriori* tests: only classes not sharing a letter differed from each other. Also Spearman rank correlation ( $r_s$ ;  $n = 71$ ) between numbers of other ants and *F. aquilonia* are given.

according to forest age (because of difficulties in classifying the fragment edges, only the fragment interiors and surroundings were included in the analyses). The best models obtained indicated that (1) the number of species depended only on the forest age the young-forest sites housing more species (Species\*Age, *Formica*; Table 5). However, it is plausible to suggest that the numbers of *F. aquilonia* reduced the number of species, because the model Species\*Age, Species\**Formica* ( $G^2 = 1.74$ ,  $df = 2$ ,  $p = 0.419$ ) differed from the more

Table 4. Numbers of sampling sites with low and high numbers (defined by medians) of species (Median = 2), *M. ruginodis* ( $M = 8$ ), and *C. herculeanus* ( $M = 0$ ) in abundance classes of *F. aquilonia* (1 = <16, 2 = 16–2000, 3 = >2000 workers in the sample;  $n = 35, 17$ , and 19 in the classes, respectively). Equality of occurrences in low and high numbers were tested with log-likelihood-ratio test ( $G^2$ ;  $df = 2$ ) or Fisher's exact test (*C. herculeanus*). (– = not tested because of scanty occurrences.)

Class:	1	2	3	$G^2$	$P$
<hr/>					
Number of spp.					
low	13	10	19		
high	22	7	0	26.82	0.000
<i>M. ruginodis</i>					
low	15	7	13		
high	20	10	6	3.88	0.144
<i>C. herculeanus</i>					
low	12	12	17		
high	23	5	2	—	0.000
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Table 5. Best models and their log-likelihood ratio statistics for the interrelations among forest age (Age, cutpoint = 80 yrs), the abundance of *F. aquilonia* (*Formica*, cutpoint = 15), and (1) numbers of other ant species (Species, cutpoint = 2), (2) abundance of *M. ruginodis* (*Myrmica*, cutpoint = 8), and (3) abundance of *C. herculeanus* (*Camponotus*, cutpoint = 0). In the models, the independence of variables is indicated by a comma (A, B), and interacting variables with an asterisk (A\*B).

Model	$G^2$	$df$	$P$
Species*Age, <i>Formica</i>	5.21	3	0.157
<i>Myrmica</i> *Age, <i>Formica</i>	1.12	3	0.772
<i>Camponotus</i> * <i>Formica</i> , Age	2.36	3	0.502



parsimonious lower-level model (Table 5) marginally significantly (difference between the two models:  $G^2 = 3.47$ ,  $df = 1$ ,  $p = 0.062$ ). The standardized deviates between the observed cell frequencies and those expected for the lower-level model indicated that the wood ants reduced the numbers of other species especially in the old forests. (2) The numbers of *M. ruginodis* depended only on forest age, their numbers being higher in the young-forest sites (*Myrmica*\*Age, *Formica*), whereas (3) the numbers of *C. herculeanus* were suppressed by the wood ant regardless of forest age (*Camponotus*\**Formica*, Age).

## 4. Discussion

Three main conclusions arise from our results: (1) The number of species in the ant community in old forests was low compared to the numbers in younger stages of forest succession. (2) A weak negative association existed between the species richness of ants and the size of the old-forest fragment. Presumably the increased proportion of edge habitats in the small fragments enabled the open-country species to inhabit parts of small fragments, thereby increasing their species richness. (3) The most important structuring force in the forest-ant communities was the occurrence of territorial wood ants (notably *F. aquilonia*), especially in the old forests.

### 4.1. Ant-community succession

Vepsäläinen & Pisarski (1982) listed four species-specific factors affecting the colonisation of land-uplift islands by ants: (1) habitat requirements, (2) dependence on other species, (3) dispersal capacity, and (4) level of social organisation (competitive status). In the following, we apply these factors in the context of forest succession following a major disturbance such as forest fire or clearcutting.

Most of the forest-dwelling ant species in our study area require sun-exposed habitats (Collingwood 1979) for instance sparse forests on rocky or barren soils (Oinonen 1956) or forests in the early stages of succession (Punttila et al. 1991). The number of ant species in a forest

stand declines rapidly after canopy closure (Oinonen 1956, Punttila et al. 1991), which in our data explains the low number of species in the closed and shady old forests.

Availability of hostess-species colonies is a prerequisite for the successful invasion by ant species which establish their colonies through temporary nest parasitism (Vepsäläinen & Pisarski 1982). Such relationships are common among forest-dwelling ants in the southern Finnish taiga (Vepsäläinen & Pisarski 1982), and thus the colonising sequence of species is to a great degree determined by the availability of hostess-species colonies. In our data, *F. sanguinea* and many species of the wood-ant group (*Formica* s. str.) are known to or assumed to establish their new colonies through temporary nest parasitism in the nests of *Serviformica* species (e.g. *Formica fusca*, *F. lemni*) (Gösswald 1951b, 1952, Kutter 1969, Hölldobler & Wilson 1990). In our study area *Serviformica* colonies are abundant in early stages of forest succession (Punttila et al. 1991, Punttila, Haila, Tukia, unpubl.), but species using them seem to differ greatly in their capability for this kind of colony founding. *F. sanguinea* queens seem to be efficient dispersers and successful colonisers (Oinonen 1956, Punttila et al. 1991), and indirect evidence — i.e. the abundance relations of the wood-ant species in young forests (Punttila 1989) — suggests that this kind of colony establishment is probably more common and/or successful in *F. lugubris* than in *F. aquilonia* (also see Rosengren and Pamilo 1983).

The exact dispersal-capacity of ant species is poorly known, with some evidence for large variability among the species (Vepsäläinen & Pisarski 1982). However, open-country forest ants in most parts of Finland are not likely to be limited by dispersal, because forest-management practices have created a dense forest-road network and a small-scale mosaic of forest stands of different ages. Both the network and mosaic provide a continuum of suitable nesting sites within the range of the dispersal capacities of even the poorest-dispersing open-country species (see also Punttila et al. 1991). This suggests that there should be no great differences in the pools of potential colonisers among different disturbed forest patches on a regional level. Isolation may, however, hamper colonisation of some mature-

forest species that spread through nest-splitting (Vepsäläinen & Wuorenrinne 1978, Punttila 1989; see next section).

Interspecific competition combined with differences in colonisation ability may be important in community succession. For instance, the efficient coloniser *F. sanguinea* seems to be more rapid than other species in spreading through nest-splitting (Oinonen 1956) and also to be better adapted to sun-exposed habitats than are most of the wood-ant species (Rosengren et al. 1979, 1986). Thus, this species may be able to slow down or even prevent the colonisation of ecologically quite similar wood ants in early stages of forest succession (Oinonen 1956, Rosengren et al. 1979, Punttila 1989, Punttila, Haila, Tukia, unpubl.). Such priority effects may also concern species of the genus *Myrmica*. In our study area, *M. ruginodis* is the only species of its genus capable of persisting in a forest stand through the whole successional cycle (Punttila et al. 1991), and it has been reported to be capable of spreading through nest-splitting (Brian & Brian 1955). *M. ruginodis* benefits from the increased insolation following clearcutting or other major disturbance (Brian & Brian 1951, Punttila et al. 1991). By effective nest-splitting it may gain competitive benefit, if it is able to monopolize the "*Myrmica* niche space" (sensu Vepsäläinen & Pisarski 1982) of the disturbed area rapidly enough (Punttila et al. 1991, Punttila, Haila, Tukia, unpubl.). Although competition is commonly an important structuring force in ant communities, many species have the ability to promote coexistence (see Savolainen & Vepsäläinen 1988, 1989, Vepsäläinen & Savolainen 1990), and competition among the top competitors may indirectly benefit the subordinate species (Rosengren 1986, Punttila, Haila, Tukia, unpubl.). Also in our data, the dominant wood ant *F. aquilonia* affected its subordinate species in various ways.

In addition, fragment size and isolation affect colonisation success. In previous studies, Punttila (1989) reported that small and isolated old-forest stands are inhabited mainly by wood-ant species, which in our study area are monogynous and monodomous, e.g. *F. lugubris* (i.e., the colony consists of a single nest; Rosengren & Pamilo 1983, Pamilo et al. 1992). Similarly, larger old-

forest fragments tend to be monopolized by multinest colonies of *F. aquilonia* spreading through nest-splitting. Vepsäläinen & Wuorenrinne (1978) found a similar distribution pattern of the wood-ant species in a forest area fragmented by urbanization in southern Finland. In the present data, however, no such effect of fragmentation was detected.

## 4.2. Effects of forestry on ant communities

Differences that most likely have changed the ant-community succession in managed forests compared to that in naturally regenerating forests include structural characteristics of the successional stands, timing of canopy closure and length of the rotation cycles. In addition, ant communities have presumably been affected by such landscape-level changes as regional changes in proportions of forest age-classes and increased proportion of edge habitats.

Major disturbances under more primordial conditions were forest fires (Zackrisson 1977, Haapanen & Siitonen 1978, Tolonen 1983, Engelman 1987) and storms (Kauhanen 1989, Esseen et al. 1992). Fire intensity, for instance, varied widely both within and among different forest stands (Kujala 1926), whereas no trees are left in clearcut areas. Clearcutting is often detrimental for wood-ant colonies as the workers lose their orientation ability, which is based on visual cues (Rosengren & Pamilo 1978 and references therein). Further, an important food resource, the aphid colonies in the trees, are destroyed through clearcutting. Compared to clearcuttings, trees supporting aphid colonies may survive the fire in less disturbed locations. In such places the ant colonies may also survive the disturbance (Punttila 1989, Punttila, Haila, Tukia, unpubl.) because of their ability in nest-splitting (Rosengren & Pamilo 1978, Vepsäläinen & Wuorenrinne 1978, Punttila 1989).

Another difference between natural disturbance and logging is the larger amount of dead and dying wood after a fire or windfall. Many ant species (e.g. *C. herculeanus*) colonise dead trunks and stumps (see Oinonen 1957). Although *C. herculeanus* colonises the exposed areas rapidly (Punttila et al. 1991), it presumably finds

fewer suitable nesting sites in clearcut areas where only the stumps are left behind. Also regular thinning results in a decreased amount of dead wood. Further, the loss of deciduous trees in managed forests may sometimes decrease the possibilities of ants to inhabit the stand. For instance, Oinonen (1958) observed that in dry pine forests in Lapland, the wood-ant mounds were most commonly found near the scattered birches that housed aphid colonies (Laine & Niemelä 1989). Similarly, according to Rosengren et al. (1979) wood-ant populations are denser in mixed forests than in pure coniferous ones.

Because tree plantations are often sparse, canopy closure occurs later than in naturally regenerating sites (Hari et al. 1982). This prolongs the time-span during which the open-country species prevail in the managed stands (Punttila, Haila, Tukia, unpubl.). As the regional proportion of young forests has increased, presumably the open-country species have benefitted. The increased proportion of edge habitats following fragmentation has resulted in the same kind of changes in the ant fauna, because open-country species may inhabit parts of the mature-forest fragments. The lengths of rotation cycles are rather standardized (70–100 yrs) in southern Finland compared to natural fire cycles (Engelmark 1987). For instance, dry, pine-dominated forests may have burnt at intervals of some dozens of years, whereas moist and isolated spruce-dominated stands may have served as fire-refuges (see Esseen et al. 1992).

Among the wood-ant group, species have presumably adapted differently to the fire regeneration of the taiga: through nest-splitting the slowly growing multinest colonies of the polygynous *F. aquilonia* may be capable of monopolizing large forest areas starting from the moister fire refuges and spreading slowly through the forests. These supercolonies are capable of excluding the colonies of other wood-ant species; thus, monodomous colonies of species such as *F. lugubris* can most often be found in poorer fire-prone stands and in isolated forest fragments which cannot effectively be colonised by *F. aquilonia* (Punttila 1989). Such differences in the habitat distribution of wood-ant species have been reported in Finland, and it has been suggested that interspecific competition is involved

(Vepsäläinen & Wuorenrinne 1978, Rosengren et al. 1979, Rosengren & Pamilo 1983, Laine & Niemelä 1989). Thus, heavily fragmented forest landscapes with large proportion of young stands become dominated by monodomous colonies of wood ants. These species, however, presumably do not have such an overwhelming impact on the forest ecosystem as does *F. aquilonia* — the huge multinest colonies of this species are capable of very efficient use of the forest patches (Rosengren & Pamilo 1983). In such supercolonies the individual nests seem to manage well even in the most shady conditions, presumably because of the supporting nest network (see Rosengren & Pamilo 1983). When management practices destroy the multinest colonies from a larger area, these ants may take a very long time to return (Rosengren et al. 1979).

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Appendix 1. Total abundances (n) and incidences (I) of worker (w) and queen (q) ants in fragment interiors, edges and surroundings. (– = not recorded.)

		Interior		Edge		Surroundings		Total	
		n	I	n	I	n	I	n	I
<i>Myrmica lobicornis</i>	w	3	1	17	2	29	10	49	13
	q	–	–	4	3	4	4	8	7
<i>Myrmica ruginodis</i>	w	189	15	455	23	650	22	1294	60
	q	10	8	17	8	36	13	63	29
<i>Myrmica scabrinodis</i>	w	–	–	1	1	17	1	18	2
	q	2	1	–	–	3	2	5	3
<i>Myrmica sulcinodis</i>	w	1	1	–	–	50	4	51	5
	q	–	–	–	–	2	1	2	1
<i>Leptothorax acervorum</i>	w	–	–	4	3	4	3	8	6
	q	–	–	–	–	1	1	1	1
<i>Formicoxenus nitidulus</i>	w	3	2	–	–	–	–	3	2
	q	3	1	–	–	–	–	3	1
<i>Camponotus herculeanus</i>	w	45	8	59	10	45	12	149	30
	q	–	–	1	1	–	–	1	1
<i>Lasius niger</i>	w	1	1	3	2	–	–	4	3
<i>Lasius flavus</i>	q	–	–	–	–	1	1	1	1
<i>Lasius umbratus</i>	q	2	2	1	1	4	4	7	7
<i>Formica fusca</i>	w	–	–	2	2	36	10	38	12
<i>Formica lemani</i>	w	–	–	4	3	39	11	43	14
<i>Formica transcaucasica</i>	w	–	–	–	–	16	1	16	1
<i>Formica uralensis</i>	w	2	2	93	2	–	–	95	4
<i>Formica rufa</i>	w	1	1	11	1	2245	2	2257	4
<i>Formica aquilonia</i>	w	54237	18	68363	16	16105	15	138705	49
	q	1	1	–	–	–	–	1	1
<i>Formica lugubris</i>	w	852	5	24	3	372	7	1248	15
<i>Formica pratensis</i>	w	–	–	–	–	22	1	22	1
<i>Formica sanguinea</i>	w	–	–	–	–	48	2	48	2
	q	–	–	–	–	2	2	2	2
Total abundance	w	55334		69036		19678		144048	
	q	18		23		53		94	
	all	55352		69059		19731		144142	
Total number of spp.	w	10		12		14		17	
	q	5		4		8		11	
	all	12		13		16		19	