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Colonisation of a burned mountain-birch forest by ants (*Hymenoptera, Formicidae*) in subarctic Finland

Abstract. We studied the colonisation by ants of a burned mountain-birch [*Betula pubescens* subsp. *tortuosa* (LEDEB.) NYMAN] forest in subarctic Finland. We recorded the post-fire ant-community succession using pitfall traps during four summer seasons following the fire. In addition, we described the vegetation of the sampling sites yearly and related it to the ant-community succession. The ant community comprised three species. The numbers of worker ants, especially of *Formica gagatoides* RUZS., decreased in the second year after the fire but later the numbers increased steadily. The numbers of queens of *Leptothorax acervorum* (FABR.), on the contrary, apparently peaked in the first year after the fire, which presumably indicated an increased colonisation rate in the burned area. The fire had destroyed the vegetation and the trees of the area almost totally, but plant succession started rapidly. There were floristic differences among the sampling sites which were attributable to altitudinal variation in the vegetation, but these vegetational differences were not detectable in the ant data. We emphasize the importance of studies on succession in extreme and labile mountain-birch ecosystems.

INTRODUCTION

Modern forestry has created successional cycles different from those that prevailed under more primeval conditions of the taiga when the main disturbances were wildfires and storms (ZACKRISSON 1977, HAAPANEN, SIITONEN 1978, TOLONEN 1983). Consequently, an important issue in conserving threatened forest species is how forestry-driven successions differ from natural ones (PUNTTILA et al. 1991). As wildfires are nowadays effectively eliminated in Finland as well as in most other European countries, it has become difficult to study natural succession in burned forests on a large scale. Since so many threatened invertebrate species in Finland are dependent on forests and a number of them also on forest fires (RASSI, VÄISÄNEN 1987), it is important to use all the possibilities to investigate the rare accidental forest fires. In the literature, there can be found a number of such studies on ground-dwelling arthropods (e.g. FORSSLUND 1951, PALM 1955, BUFFINGTON 1967, BUCK 1979, SCHAEFER 1980, HAUGE, KVAMME 1983, LUNDBERG 1984, KOPONEN 1988a,b, 1989, HOLLIDAY 1991).

Some data exist about direct effects of fires on ants and on their community succession after fire (BRIAN et al. 1976, SPRINGETT 1976, MAJER 1980, WHELAN et al. 1980, O'DOWD, GILL 1984, ANDERSEN, YEN 1985, DONNELLY, GILIOMEE 1985, PUNTTILA et al. 1991), and after forest cutting or afforestation (e.g. SZUJECKI et al. 1977, 1978, PUNTTILA et al. 1991, 1993a, PUNTTILA 1993). The social mode of life makes ants different from solitary organisms in terms of colonisation processes in the early phases of succession (VEPSÄLÄINEN, PISARSKI 1982, PUNTTILA et al. 1991, 1993a). During the colonisation stage the role of stochasticity is restricted because many species-specific factors, including habitat requirements, dispersal and competitive capacities, mode of colony founding, and the level of social organisation are more important.

In this paper we summarize data on changes recorded in an ant assemblage of a mountain-birch forest after fire. We focus on the immediate effects of fire on ant colonies and the response of an ant-community to plant succession following a fire.

MATERIAL AND METHODS

Study area and habitat structure

The field work was carried out in Kevo Lapland, northern Finland (69°36'N, 26°52'E; Fig. 1), in the valley of the river Kevo. For detailed climate and vegetation descriptions of the area see KÄRENLAMPI (1972) and HÄMET-AHTI (1963). In July 1985, an area of ca. 30 ha of open forest of ca. 2–3 m tall mountain-birch [*Betula pubescens* subsp. *tortuosa* (LEDEB.) NYMAN] burned in a river canyon in Kevo Strict Nature Reserve (see KOPONEN 1989). The vegetation, including the trees, of the area was burned down and the site of the fire covered a part of the plateau along the banks of the river Kevo (at 120 m a.s.l.) and the steep slopes (up to 220–240 m a.s.l.) of the mountain Salteroavvi.

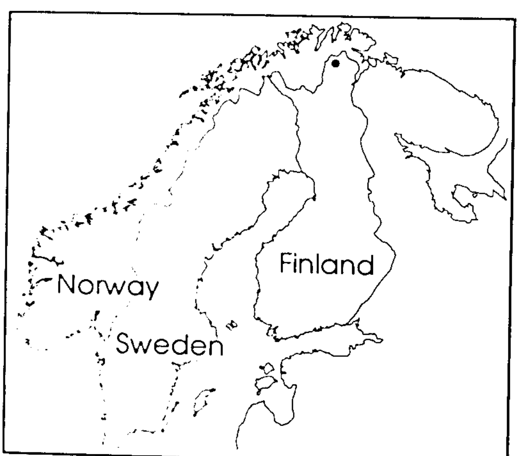

Fig. 1. Location of the study area in Kevo Lapland, northern Finland.

The vegetation was described around each of the 60 traps (see below) using 1 m^2 quadrats, in which the proportional coverage of vascular plants, mosses and lichens was estimated. For the burned sites, the vegetation was described yearly.

Sampling design

We sampled invertebrates by pitfall traps (see PISARSKI et al. 1982, PUNTTILA et al. 1991) during four summer seasons following the fire. We sampled ants in five sites on the river plateau and in two sites on the mountain slopes, with two and one sites, respectively, as controls in similar unburned sites. In each site, we used six traps placed at ca. 2 m intervals in two lines (60 traps in all). All sampling sites in the burned area were situated at a ca. 50 m distance from the border of the unburned area as were the control sites on the other side of the border. The traps were glass jars (60 mm in diameter, 80 mm deep) covered by raised metal roofs and filled to $^1/_4$-$^1/_3$ with ethylene glycol and detergent. The trapping periods covered ca. two months from the end of June through the end of August in 1986–1989. The ants were identified by M. SAARISTO.

Statistical analyses

We used two-way indicator species analysis (TWINSPAN; HILL 1979) to classify the sampling sites according to their vegetation characteristics and detrended correspondence analysis (DCA; HILL, GAUCH 1980) to identify important environmental gradients and reveal successional trends in our study area. We analysed the effects of vegetation variation on the distribution of ants using the classes obtained by the TWINSPAN method. The ant data were analysed using Fisher's exact tests for two-by-four tables (StatXact statistical software).

RESULTS

Habitat structure and plant succession

The fire affected the vegetation and top soil of the sampling sites severely, except in one site where ca. 10% of the vegetation remained undamaged. In 1986, the first year after the fire, a 0.5–1.0 cm thick layer of charcoal and ash covered the area, and the sites almost entirely lacked vascular plants and mosses (Table 1). However, both mosses and herbs reappeared rapidly, although the vegetation differed a lot from the control sites throughout the study period. In a DCA-ordination of the vegetation of the sampling sites, the first axis was related to plant succession (Fig. 2). The distance between the burned and control sites increased along this axis year by year. The second axis reflected floristic differences between the mountain slopes and the river plateau. This difference was still clear after the fire. The main difference in the vegetation between the mountain slopes and the river plateau was that the coverage of the grass *Calamagrostis lapponica* (WAHLENB.) HARTMAN was higher on the mountain-slope. Plant succession started rapidly with the mosses *Ceratodon purpureus* (HEDW.) BRID. and *Polytrichum* HEDW. spp. Also *C. lapponica* increased in coverage, whereas dwarf shrubs, such as species of the genera *Arctostaphylos* ADANSON, *Empetrum* L. and *Vaccinium* L., mosses *Hylocomium* SCHIMP. sp. and

Pleurozium MITT. sp., and lichens present in the control plots did not increase markedly in coverage in the burned area during the study period.

Table 1. Mean coverages of floristic components of the sampling sites in 1986–1989. Also the coverages of some important species are given: RP – river plateau, MS – mountain slope, – – no data (vegetation of the control sites was not described every year); the minimum coverage of a species is indicated by 1, thus the values in the table overestimate the actual coverages slightly

Year	Vegetation	Burned sites							Control sites		
		RP					MS		RP		MS
		1	2	3	4	5	9	10	6	7	8
1986	Herb layer	5	2	2	2	1	4	5	59	59	74
	Calamagrostis lapponica	0	1	0	0	0	3	4	0	2	1
	Moss layer	3	1	1	0	0	1	1	42	31	25
	Ceratodon purpureus	0	0	0	0	0	0	0	0	0	0
	Polytrichum spp.	1	1	1	0	0	1	1	9	1	1
	Lichens	6	0	0	0	0	0	0	6	2	4
1987	Herb layer	9	3	2	2	2	18	12	58	56	–
	Calamagrostis lapponica	0	2	0	0	0	16	10	0	2	–
	Moss layer	10	5	7	15	9	14	8	41	31	–
	Ceratodon purpureus	1	4	5	14	9	14	8	0	0	–
	Polytrichum spp.	8	1	2	1	0	1	1	8	1	–
	Lichens	19	1	1	0	0	0	1	6	3	–
1988	Herb layer	9	4	3	2	2	25	22	–	–	–
	Calamagrostis lapponica	0	2	0	0	0	24	20	–	–	–
	Moss layer	19	11	22	33	34	29	19	–	–	–
	Ceratodon purpureus	1	10	18	33	33	28	19	–	–	–
	Polytrichum spp.	17	1	4	1	1	1	1	–	–	–
	Lichens	20	1	1	0	0	0	1	–	–	–
1989	Herb layer	14	7	5	4	3	29	29	58	47	66
	Calamagrostis lapponica	0	3	0	0	0	27	27	0	2	2
	Moss layer	23	30	34	43	48	40	47	45	39	29
	Ceratodon purpureus	1	28	26	41	46	38	45	0	0	0
	Polytrichum spp.	20	1	8	2	2	1	2	8	1	1
	Lichens	19	1	0	0	0	0	0	7	4	6

In the first division of the TWINSPAN classification of the vegetation of the sampling sites, the control sites were separated from the burned ones (Fig. 3). This division was indicated by the moss *C. purpureus* in the burned sites. In the second division, the one less severely burned site was separated from the rest of the burned ones [indicated by the dwarf shrub *Empetrum nigrum* subsp. *hermaphroditum* (HAGERUP) BÖCHER], which, in turn, were divided into river-plateau and mountain-slope sites in the next division (indicated by *Polytrichum* mosses in the mountain-slope sites).

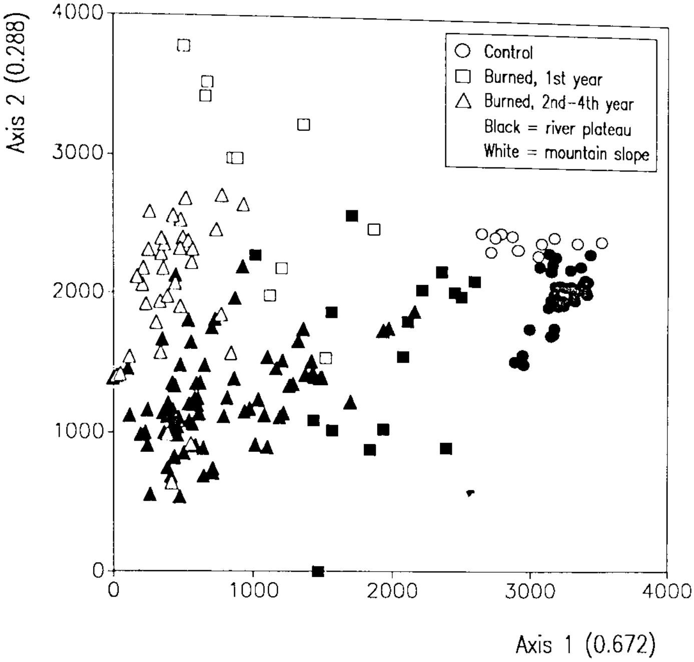

Fig. 2. The sampling sites of the burned areas and control ones plotted on the 1st and 2nd axis of detrended correspondence analysis according to their plant cover. The eigenvalues of the axes are shown in parentheses.

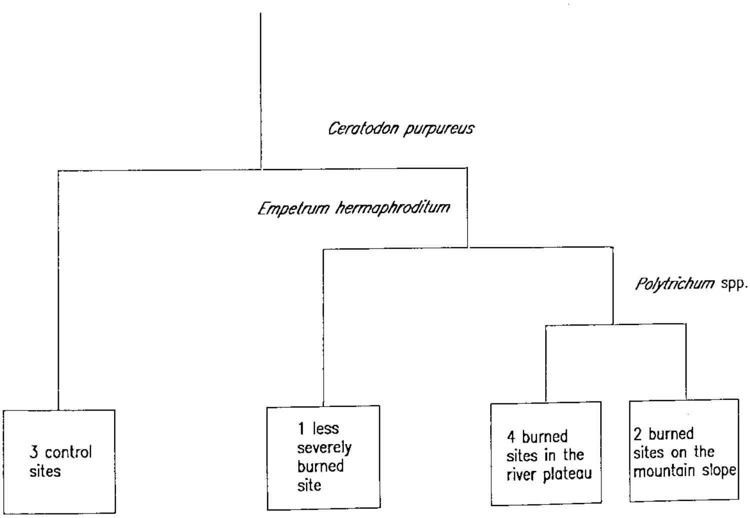

Fig. 3. The TWINSPAN classification of the sampling sites according to their vegetation characteristics. The indicator species of the divisions are also given.

Ants in the burned area

The total number of ants sampled was 213 workers and 49 queens belonging to three species (Table 2). The catches included workers of two species, *Leptothorax acervorum* (FABR.) and *Formica gagatoides* RUZS., whereas *F. aquilonia* YARR. was represented by three queens.

Table 2. The total samples of worker and queen ants in the ten sampling sites in 1986–1989: RP – river plateau, MS – mountain slope, w – workers, q – queens

Year	Species		Burned sites							Control sites		
			RP					MS		RP		MS
			1	2	3	4	5	9	10	6	7	8
1986	*Leptothorax acervorum*	w	4	–	10	1	–	–	–	–	–	4
		q	–	1	5	7	6	1	4	1	–	–
	Formica gagatoides	w	2	–	41	12	4	1	3	3	–	3
	Formica aquilonia	q	–	–	–	–	–	–	–	–	–	–
1987	*Leptothorax acervorum*	w	–	–	–	–	1	–	–	1	1	–
		q	1	–	–	–	–	1	–	–	–	1
	Formica gagatoides	w	–	–	–	1	2	–	2	5	–	1
	Formica aquilonia	q	–	–	–	–	–	–	–	–	–	–
1988	*Leptothorax acervorum*	w	1	–	–	1	–	–	–	1	–	–
		q	–	1	1	3	2	–	6	1	–	–
	Formica gagatoides	w	–	–	–	4	2	–	3	7	–	5
	Formica aquilonia	q	–	–	–	–	–	–	2	–	–	–
1989	*Leptothorax acervorum*	w	2	–	1	–	–	–	–	5	–	–
		q	–	1	–	–	1	–	1	1	–	–
	Formica gagatoides	w	2	4	4	11	8	1	4	25	1	19
	Formica aquilonia	q	–	–	–	–	–	–	1	–	–	–

Both *L. acervorum* and *F. gagatoides* workers were more abundant early in the season (Fig. 4). In the burned area, their numbers decreased after the first year following the fire, but increased steadily in the subsequent years (Fig. 5). However, the difference between the burned sites and controls was statistically significant only for *F. gagatoides*. The numbers of *L. acervorum* queens were higher earlier in the season, except in the first year after the fire (Fig. 4). In the burned area, their numbers peaked in the first and the third year after the fire, although the difference between the burned sites and controls was not statistically significant (Fig. 5).

The numbers of workers of either *L. acervorum* or *F. gagatoides* did not differ among the habitat classes obtained by the TWINSPAN method and the result was similar also for *L. acervorum* queens (Fig. 6). In the latter case, this was presumably attributable to the small sample size, because when we classified the sites according to the first division of the TWINSPAN classification, *L. acervorum* queens tended to be more abundant in the burned sites (Fisher's exact test, $p = 0.084$).

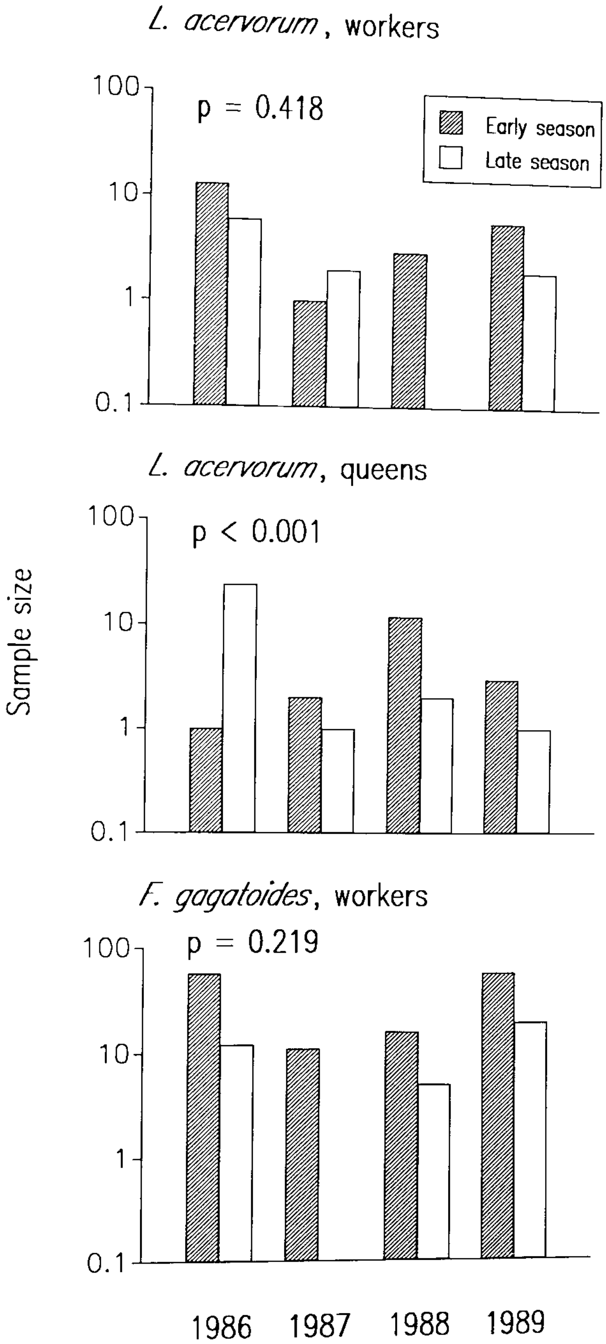

Fig. 4. The pooled catches of ants in the early and late seasons in 1986–1989. The Fisher's exact test statistics are also given.

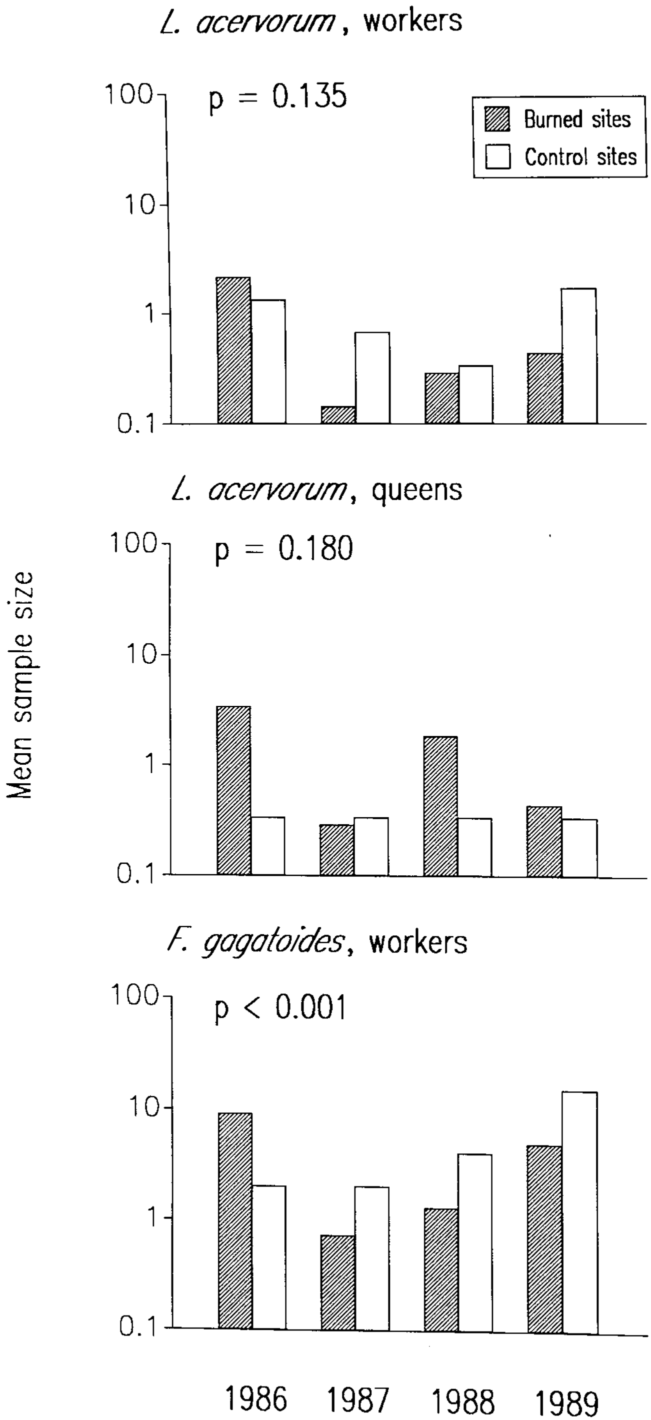

Fig. 5. The mean catches of ants in the burned and control sites in 1986–1989. The Fisher's exact test statistics are also given.

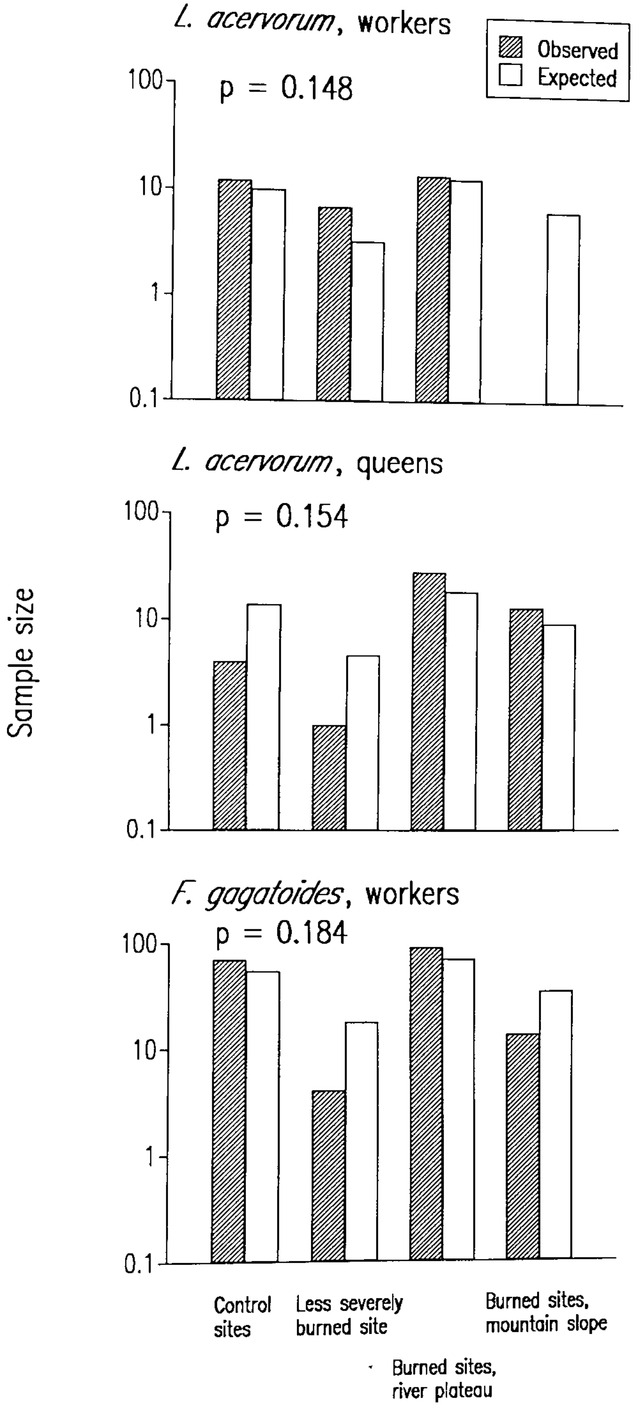

Fig. 6. The observed and expected numbers of ants in the habitat classes obtained by the TWINSPAN method. The expected numbers were calculated on the basis of the number of samples in each class. The Fisher's exact test statistics are also given.

DISCUSSION

Direct effects of fire

Direct destruction of ant colonies by fire probably was not the most important reason for the decrease in the numbers of *F. gagatoides* workers in the burned area, as the heat did not necessarily reach deep into the soil (cf. VASANDER, LINDHOLM 1985) where the chambers of at least larger ant colonies lie. Instead, as the vegetation is destroyed, food shortage following the fire may be of greater importance for such species which are dependent on aphids (BRIAN 1955, PUNTTILA et al. 1991). In our data, the numbers of *F. gagatoides* workers fell in the second year following the fire, which might have reflected this. In other studies on the effects of fire on ants, the number of species as well as the abundance or activity of species increased after the fire (SPRINGETT 1976, MAJER 1980, WHELAN et al. 1980, O'DOWD, GILL 1984) or the effect of the fire varied according to the species concerned (BUFFINGTON 1967, ANDERSEN, YEN 1985). In many of these studies, the ants started to exploit the heavy seed fall after the fire.

Colonisation and succession

Queens of only two species, *L. acervorum* and *F. aquilonia*, were included in our data. The numbers of *L. acervorum* queens peaked in the first (and the third) year following the fire, which may have indicated colonisation attempts into the newly burned area. In addition to being able to select suitable nesting habitats in flight (cf. BRIAN 1952, PONTIN 1960, BRIAN et al. 1966, WILSON, HUNT 1966, PUNTTILA et al. 1991), ant queens may walk to a given area because not all young queens found new colonies in the first year of their life. PUNTTILA et al. (1991) found out that individual *L. acervorum* queens can be found wandering around at any time of the growing season, which may indicate that they are trying to find established colonies which they could join or that they are trying to found new colonies by themselves. Burned areas appear to be optimal habitats for *L. acervorum*: queens seem to find suitable sites for colony founding in cones, sticks, stumps and under stones revealed under the moss layer after the fire, as well as in developing moss tussocs (PUNTTILA, unpubl. data from more southern latitudes), and they are also known to nest in pieces of burned wood (SAARISTO, pers. observ.), e.g. in burned birch stems which were abundant in our study area. In the first year following the fire, the numbers of *L. acervorum* queens were high especially later in the season, i.e. at the swarming time of the alatae, supporting our suggestion of colonisation attempts. The absence of *F. gagatoides* queens in our samples was presumably attributable to the nest-founding strategy of the species: queens start new colonies alone and dig their nesting cavities immediately after they have landed from their nuptial flight (cf. PUNTTILA et al. 1991). Thus, they cannot be caught effectively into pitfall traps. Most species of the wood-ant group (*Formica* s.str.) are typical inhabitants of later successional stages (BRIAN 1983, PUNTTILA et al. 1991, 1993a, PUNTTILA 1993) and hence, our study period was much too short for their colonisation. The exposition of our sampling sites, however, indicates that these sites cannot be inhabited by wood ants (see LAINE, NIEMELÄ 1989, K. KARHU, pers. comm.).

The observed increase in the numbers of *L. acervorum* and *F. gagatoides* workers may have resulted either from the growth of colonies damaged but not destroyed by the fire, or from new colonisations to the area. In the first years of their life, ant colonies grow very slowly. Thus, even a high density of incipient colonies is reflected in pitfall-trap data only after some years, which in our material presumably was the case at least for *L. acervorum* (PUNTTILA, unpubl. data from more southern latitudes). In addition, the foraging ranges of *L. acervorum* workers are very short (BRIAN et al. 1965). The numbers of both *L. acervorum* and *F. gagatoides* workers increased slightly also in the control sites during our study period. This may have reflected either true population growth, or an effect of annual weather conditions or colony removals from the more severe post-fire conditions in the burned area. However, the latter explanation seems less plausible as the distances between the control sites and the burned area were ca. 50 m.

The vegetation of the burned sites suffered from arid conditions late in the season, which may have been the main reason for the low activity of the ants then. The exceptionally cold and rainy weather conditions in 1987 may also have affected the activity of ants, but it is not clear whether this effect could still be seen after two years.

The ant communities of mature mountain-birch forests are dominated by species belonging to the wood-ant group (*F. aquilonia*, *F. lugubris* ZETT. and *F. truncorum* FABR.) in river valleys and at lower elevations on mountain slopes (VEPSÄLÄINEN et al. 1984, LAINE, NIEMELÄ 1989). Other abundant ant species in Kevo area include *Myrmica ruginodis* NYL., *M. sulcinodis* NYL. and *F. exsecta* NYL. (VEPSÄLÄINEN et al. 1984). However, only three ant species were represented in our data, which may reflect the patchiness of the distribution of ant species under harsh and unpredictable subarctic conditions. The patchy distribution may be caused by, e.g. unfavourable exposition (see LAINE, NIEMELÄ 1989). Also the other data sets of invertebrates collected in Kevo by KOPONEN (1971) and KOPONEN, OJALA (1975) lacked ants almost entirely.

In the colonisation of newly burned or clearcut forests in more southern latitudes, the mode of colony founding of ant species seems to affect the sequence in which the species colonise the areas (PUNTTILA et al. 1991, 1993a). Pioneering species are capable of independent colony founding, and they are followed by species which establish new colonies through temporary nest parasitism. Later, when the densities of colonies and, hence, the densities of foraging ant workers are high, presumably the only way to found new colonies is through nest budding, which leads to a polydomous or polycalic colony structure (PUNTTILA et al. 1991, 1993a). In our data too, the pioneering species, *L. acervorum* and *F. gagatoides*, belong to the first group (independent colony founding), whereas *F. aquilonia* belongs to the last group (mainly step-by-step dispersal through nest budding; cf. ROSENGREN, PAMILO 1983).

In mature subarctic birch forests the wood ants, especially *F. aquilonia*, are important in restricting moth outbreaks. Some geometrid moths have mass outbreaks in these forests approximately at ten-year intervals (TENOW 1972), and the wood ants have been shown to prevent or lower the damage and the numbers of herbivores on the birches within their territories (LAINE, NIEMELÄ 1980, 1989, PUNTTILA et al. 1993b,c). Thus, further studies on ant-community succession are needed to explore the birch-herbivore-ant dynamics in more detail under subarctic conditions.

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STRESZCZENIE

Zasiedlanie przez mrówki (*Hymenoptera, Formicidae*) spaleniska w górskim lesie brzozowym w subarktycznym regionie Finlandii

Badano sukcesję zgrupowań mrówek w spalonym górskim lesie brzozowym (*Betula pubescens* EHRH. ssp. *tortuosa*) w północnej Finlandii. Zmiany w myrmekofaunie rejestrowano za pomocą pułapek Barbera w ciągu 4 kolejnych sezonów po pożarze. Rokrocznie też opisywano roślinność stanowisk badawczych, odnosząc jej stan do przebiegu sukcesji mrówek. Badany zespół mrówek liczył 3 gatunki: *Leptothorax acervorum* (FABR.), *Formica gagatoides* RUZS. i *F. aquilonia* YARR. Liczebność robotnic mrówek, zwłaszcza *F. gagatoides*, zmniejszyła się w drugim roku po pożarze, po czym znacznie wzrosła. Liczebność królowych *L. acervorum* natomiast zwiększyła się w pierwszym roku po pożarze, co prawdopodobnie było wyrazem wzmożonej kolonizacji świeżo zniszczonego obszaru. Pożar niemal całkowicie zniszczył wszelką roślinność, lecz sukcesja roślinna rozpoczęła się szybko i gwałtownie. Roślinność poszczególnych stanowisk różniła się między sobą, co wynikało zapewne z różnic w wysokości ich położenia. Zróżnicowanie to jednak nie wykazywało związku ze stanem myrmekofauny. Autorzy podkreślają znaczenie badań nad sukcesją biologiczną w skrajnych i labilnych ekosystemach, jakimi są górskie lasy brzozowe.