

Colonisation of a Burned Forest by Ants in the Southern Finnish Boreal Forest

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The colonisation of a burned clearcut by ants in southern Finland was monitored using pitfall traps, artificial nest sites, and direct nest sampling from the ground and stumps. Clearcutting and fire seemed to have destroyed wood-ant colonies (*Formica rufa* group), and also other mature-forest species suffered from fire. *Myrmica ruginodis* was able to survive only in less severely burned moist sites, whereas it benefitted from the enhanced light conditions in a non-burned clearcut. The fire resulted in an essentially ant-free terrain into which pioneering species immigrated. The mortality of nest-founding queens appeared to be high. The results supported the hypothesis that the pioneering species tend to be those that are capable of independent colony founding, followed by species founding nests through temporary nest parasitism. The succession of the burned clearcut differed from that of the non-burned one, suggesting that habitat selection in immigration and priority effects, i.e. competition, introduce deterministic components in the successional pathways of boreal ant communities.

Keywords forest fires, succession, competition, ant communities, boreal forests

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1 Introduction

A major issue in planning conservation of forest-dwelling organisms is how successional cycles in managed forests differ from those in more natural conditions (Hansen et al. 1991, Hansson 1992, Haila 1994, Haila et al. 1994). In managed forests, the most common disturbances include

thinnings and clearcutting, whereas the natural disturbances in primeval taiga are wildfires, storms, flooding, insect outbreaks, and snow damage (Esseen et al. 1992). Especially the role of fire has been important, and its effects were visible in the whole successional cycle of forest stands (e.g. Zackrisson 1977, Wikars 1992). Many boreal-forest organisms have become threatened in Finland because of elimination of

wildfires and promoting certain management practices like successive thinnings, planting with conifers, favouring monocultures and shortened rotation times (Heliövaara and Väisänen 1982, Rassi and Väisänen 1987).

Studies comparing natural and managed forest successions are difficult to make because natural succession does not exist or is extremely rare in managed forests. Zackrisson (1977) found that about 1 % of forest stands were affected by fire in his study area each year in northern Sweden from 1551 to 1875. In contrast, nowadays efficient fire suppression has reduced the forest area burned to only some hundreds of hectares in Finland each year (Aarne 1995). Further, these occasional fire areas are normally cleared and artificially regenerated. In the second half of the 1950's and the 1960's, the mean area prepared for forest regeneration by prescribed burning was about 19000 ha in Finland each year, but since then also the area of such burnings has been reduced to only ca. 1700 ha yearly (Aarne 1995).

Prescribed burning might mimic wildfire disturbance with a number of limitations concerning the colonisation and succession of forest organisms. For instance, in prescribed burning the clearcuts are left for drying for some time before the burning and thus, many open-country species have time to colonise the area (Niemelä et al. 1996). These species often survive from fire, and they may prevent the colonisation of specialized fire-dependent species (Wikars 1995). Further, much smaller amount of surviving, dying and dead trees are left behind in burned clearcuts as compared with the situation after wildfires. This may be crucial for many saproxylic invertebrates requiring such disturbed habitats (e.g. Muona and Rutanen 1995, Kaila et al. 1996).

However, also prescribed burning causes the colonisation, survival and succession of forest organisms to differ from those following mere clearcutting. If there are such differences as regards the disturbance type concerning keystone species (i.e. species which have disproportionately large ecological effects on other organisms; Paine 1995), burning may have far-reaching consequences in the succession and functioning of the forest ecosystem. In boreal forests, keystone species potentially showing such dif-

ferences in colonisation or survival and succession as regards to disturbance type may be found among trees, mycorrhizal fungi, soil microbes, soil invertebrates, and ants. All these groups include species which have great impact on a large variety of other organisms and processes in forest ecosystems (for ants, see references in Punttila et al. 1994). For instance, in boreal ants, the colonisation process and community succession have been suggested to include a number of rather deterministic components (Vepsäläinen and Pisarski 1982). Thus, priority effects (competitive gain from being the first to arrive) in colonisation and early community succession among keystone species may have long-lasting effects in the forest ecosystem (Punttila et al. 1994, Punttila 1996).

Studies dealing with the effects of fire on ants and ant-community recovery or succession after fire are numerous from various open fire-prone environments, e.g. grasslands, shrublands and heaths (see the reviews by Ahlgren 1974, Lyon et al. 1978, Warren et al. 1987). Although such studies are also available from many forested environments, e.g. various Australian *Eucalyptus* forests (see the review by Christensen and Abbott 1989), different types of tropical forests (e.g. Bentley 1976, Morais and Bentley 1988, Andersen 1991, MacKay et al. 1991), and various kinds of coniferous forests (e.g. Heyward and Tissot 1936, Pearse 1943, Whitford and Gentry 1981), knowledge from the Eurasian boreal zone seems to be scarce (but see Oinonen 1956, Punttila et al. 1991). In boreal ant communities, Punttila et al. (1991) found that among the colonising species, the first-coming pioneers were those that are capable of independent colony founding. These were followed by species which establish new colonies through temporary nest parasitism in the nests of other ant species. After the area has become crowded with ant colonies and foraging workers, the only possible mode of colony founding presumably is nest splitting, i.e. budding of the established colonies.

In this paper, we focus on three topics: (1) What are the direct effects of fire on ant communities in the boreal forest, (2) How are the burned areas colonised by ants, and (3) How does the community succession proceed after the fire.

2 Material and methods

We collected four separate data sets: (1) A comparison of ant communities among clearcut areas (one area subject to prescribed burning and one non-burned clearcut of the same age, 2 yrs, in the beginning of the study) and mature-forest controls in Hyytiälä, northern Häme (for the description of the study area, see Punttila et al. 1991). The areas were monitored for five years (1989–1993) with pitfall traps (plastic cups with a diameter of 65 mm, and a volume of 170 ml, partially filled with 20 % ethylene glycol and detergent, and covered with plastic non-transparent roofs). The trapping was conducted in 14-day periods twice a year (June and August, except in 1989, when both periods were in July) in four sites separated by 50–100 m with four sets of 13 traps deposited in a circle with a diameter of ca. 4 m. In the mature-forest controls, only one set of 13 traps was used in each of the two stands. The monitoring started in the first year after burning. The sampling effort was divided into two periods because of a seasonal turnover in spider and carabid species that were also included in the study. The ants were identified using the keys of Dlusskij and Pisarski (1971), Collingwood (1979) and Douwes (1981).

(2) The same burned clearcut was supplied with dark red brick plates (0.5 × 12.5 × 12.5 cm) to serve as artificial nest sites mimicking flat stones favourable for ant colonies (Brian 1952a, Oinonen 1956). The plates were placed in 6 plots separated by 50 m, each having 4 sets of 9 plates in a grid with 3 m distances, the sets being separated by 15 m (216 plates altogether). The plates were deposited in elevated dry locations, and the soil was dug to ensure that the spot was suitable for ants, and shading vegetation was removed (this was repeated during each inspection). The plates were checked for their inhabitants late in each season. In the two first years, an additional checking was done before the nuptial flight of most of the species in order to record the winter survival of the queens and colonies, whereas the late-season checkings were done after the nuptial flight of most of the species each year. These data were gathered for four years (1989–1992).

(3) We also sampled nests from 24 randomly

chosen pine and spruce stumps in two 1-ha squares in the burned clearcut. New stumps were explored each year. The stumps were explored carefully and all the soil (some of the stumps were partly covered by soil because of forestry activities) and bark on the above-ground part of the stumps were removed, and the crevices and soft parts were inspected. These data were gathered for four years (1989–1992) in the early autumn.

(4) In the vicinity of the stump samples, we took a random soil sample at 1-m distance from the stump (0.5 × 0.5 m sample square) from which we searched ant queens and colonies. The soil-sample square was dug up (5–10 cm deep depending on the soil), and all the sticks and cones within the square were explored carefully. These data were gathered for four years (1989–1992) in the early autumn.

We used detrended correspondence analysis (DCA, Ter Braak 1987) to reveal major ecological gradients in the pitfall-trap data. The analysis was performed without transformations for incidence data of combined catches of the two sampling periods for each year, and the same weight was given to all species. Detrending was done by 10 segments. DCA was performed with CANOCO statistical software (Ter Braak 1987).

3 Results

3.1 The ant fauna

The pitfall-trap data comprised 12647 worker ants and 278 ant queens belonging to 14 and 12 species (16 species altogether), respectively (Appendix). The other methods did not yield observations of any additional species (Table 1). The most abundant species in the study areas according to the pitfall-trap samples were *Formica aquilonia*, *F. sanguinea*, *Myrmica ruginodis*, *Lasius niger*, *M. sulcinodis*, and *Camponotus herculeanus*, whereas the most frequently recorded species were *M. ruginodis* (found in 514 of the 1300 samples), *F. sanguinea* (190), *L. niger* (142), *F. aquilonia* (141), *C. herculeanus* (85), and *M. sulcinodis* (72).

Table 1. Records of live (lq) and dead (dq) ant queens and colonies (c) in stumps, artificial nest sites (plates), and soil-sample squares in 1989–1992.

		Stumps				Plates				Soil			
		89	90	91	92	89	90	91	92	89	90	91	92
<i>M. lobicornis</i>	c	–	–	–	–	–	1	1	1	–	–	–	–
<i>M. ruginodis</i>	lq	–	–	–	1	–	–	–	–	–	–	–	2
	c	2	–	–	–	–	–	6	4	–	–	–	–
<i>M. scabrinodis</i>	lq	–	–	–	–	–	–	–	–	–	–	1	–
<i>M. sulcinodis</i>	lq	–	–	–	–	–	–	–	1	1	–	–	–
	c	–	–	–	–	–	–	1	6	–	–	1	–
<i>L. acervorum</i>	lq	–	–	–	–	–	1	–	–	–	–	–	–
	c	–	–	2	4	–	1	–	6	–	–	4	9
<i>C. herculeanus</i>	lq	9	5	3	2	–	–	–	–	–	–	–	–
	dq	15	2	7	5	–	–	–	–	–	–	–	–
	c	1	2	9	3	–	–	1	2	–	–	–	–
<i>L. niger</i>	lq	4	1	1	–	11	21	8	–	–	–	1	–
	dq	–	–	–	–	–	–	1	–	–	–	–	–
	c	1	2	2	2	–	1	3	5	–	–	–	–
<i>F. fusca</i> -group	lq	1	–	–	–	–	–	–	–	–	–	–	–
	c	–	–	–	–	–	–	–	4	–	–	–	–
<i>F. sanguinea</i>	c	–	–	–	–	–	–	–	1	–	–	–	–

3.2 Effect of fire on ants

In the comparison of burned and non-burned clearcuts, the burned clearcut yielded very low catches in the two first study years as compared with the non-burned clearcut and the controls (Appendix). Of the four species frequently present in mature forests, i.e. *M. ruginodis*, *C. herculeanus*, and the wood ants *F. aquilonia* and *F. lugubris* (see Niemelä et al. 1996), only two species occurred frequently enough to allow statistical testing. The incidences of both *M. ruginodis* ($X^2 = 47.25$, $df = 2$, $p < 0.001$) and *C. herculeanus* ($X^2 = 7.27$, $df = 2$, $0.001 < p < 0.05$) deviated significantly from those expected on the basis of the distribution of the sampling effort among the three treatments. Standardized deviates ((observed-expected)/expected) revealed that the incidences of both species were unexpectedly low in the burned clearcut. Thus assuming that prior to the treatments the numbers of these ants were approximately similar in all the study forests, both species, and especially *C. herculeanus*, had suffered from the burning. *M. ruginodis* seemed to have survived the fire to some extent in moist sites (pers. obs.). Based on the occurrence of

colonies of wood ants in close vicinity to the treatment forests (and thus, most likely also in the treatment forests prior to the treatments), the wood-ant colonies were presumably destroyed by clearcutting and fire.

3.3 Colonisation of the burned clearcut

The stumps were colonised rapidly by *C. herculeanus* queens which started egg laying in small selfmade chambers or tunnels of cerambycid larvae under or in the bark (Table 1). The numbers of the queens were high in the first years following the fire and rapidly decreased later on during succession. However, the success of their nest-founding attempts was quite low, as we found many dead queens in the chambers (48 queens, 29 of which were dead when found, vs 15 surviving colonies). A few successful queens had established their colonies already in the two first study years (the colonies consisted of 1–5 small workers). The size of the colonies grew in subsequent years, and some of them had up to a couple of dozens workers in the last monitoring year.

The artificial nest sites experienced a similar colonisation by *L. niger* queens as did the stumps by *C. herculeanus* queens (Table 1). Most of the colony-founding attempts were unsuccessful under the nest plates (altogether 41 observed *L. niger* queens one of which was dead when found, and only five live colonies in the last monitoring year). In the two first years, we checked the artificial nest sites also in the early season. In 1989, no nests were established by July 20, whereas in May 16, 1990, two *M. sulcinodis* and one *L. acervorum* queens were found. None of the 11 *L. niger* queens present in the late season in 1989 were found again. However, we cannot exclude the possibility that the queens left the plates and moved into more favourable locations nearby. Unfortunately, we did not use glass plates between the soil and the plate as did Brian (1952b) to minimize the disturbance of the monitoring the queens and colonies. Later on, the plates were also colonised by other species, e.g. four Myrmicines (in addition to *F. fusca* L.-group species). Especially *M. sulcinodis* was abundant in the last year monitored. The *M. ruginodis* colonies, having been quite large, presumably moved under the plates from elsewhere, but in *M. sulcinodis*, all the colonies were incipient ones. In the last year monitored, we found also one incipient colony of the slavemaking ant, *F. sanguinea*, a species that employs temporary nest parasitism in colony founding (the colony consisted of a dozen *F. fusca*-group workers and three *F. sanguinea* workers).

The soil samples, on the contrary, yielded very few queens and colonies (Table 1). Only in the third and fourth year we found a notable number of colonies of *L. acervorum*. This species has been reported to colonise also hard stumps (Brian 1952a). Franch and Espadaler (1988) studied also the hard parts of stumps, but only four of the 60 colonies found were located there. Later on, when the stumps decay, colonies of most species become very common also in the soil (pers. obs. from nearby older clearcuts and burned areas).

In addition to the nests sampled, we found two *F. aquilonia* colonies in the burned clearcut. One rather big mound was located close to the edge of the burned clearcut, and a small colony situated in a moist depression in the burned clearcut. The latter nest was similar to new bud nests of

multinest colonies and we presume that it was a bud nest of the bigger colony (clearcutting often results in nest splitting in polygynous, i.e. multi-queened, wood ants; Rosengren and Pamilo 1978). However, at least the bigger colony had survived because of active watering by the employees during the burning procedure (Henrik Lindberg, pers. comm.).

The pitfall-trap data revealed that the numbers of queens of *M. ruginodis* increased in the burned clearcut, whereas they were constantly high in the non-burned clearcut after the two first years (Appendix). Thus, if compared with the trends in the numbers of workers, *M. ruginodis* presumably colonised the burned clearcut through nest budding, and reached the density of the non-burned one only in the last study year (Fig. 1, Appendix). Also the unexpectedly high incidence of *M. ruginodis* workers in the non-burned clearcut as compared with the controls in the first study year suggest rapid spreading through nest budding following clearcutting. The congeneric *M. sulcinodis*, on the contrary, seemed to have immigrated the burned clearcut from the surroundings (pers. obs. of many incipient colonies), whereas the non-burned clearcut remained uncolonised by this species (Appendix, Fig. 1). The numbers of queens of *C. herculeanus* were higher in the non-burned clearcut than in the burned one.

3.4 Community succession in burned vs non-burned clearcuts

The pitfall-trap catches of many of the species increased especially in the burned clearcut during the five study years (Fig. 1, Appendix). The DCA-ordination showed that the communities of the open clearcuts differed from those of the mature forests, and that the community of the burned clearcut diverged from that of the non-burned one, indicating different successional pathways between these areas (Fig. 2). The burned clearcut was characterized by colonisation of *M. sulcinodis* and slightly higher numbers of *L. acervorum* than in the non-burned clearcut, whereas *F. sanguinea* and *L. niger* prevailed in the non-burned clearcut already in the first study year (Fig. 3). *M. ruginodis* was present

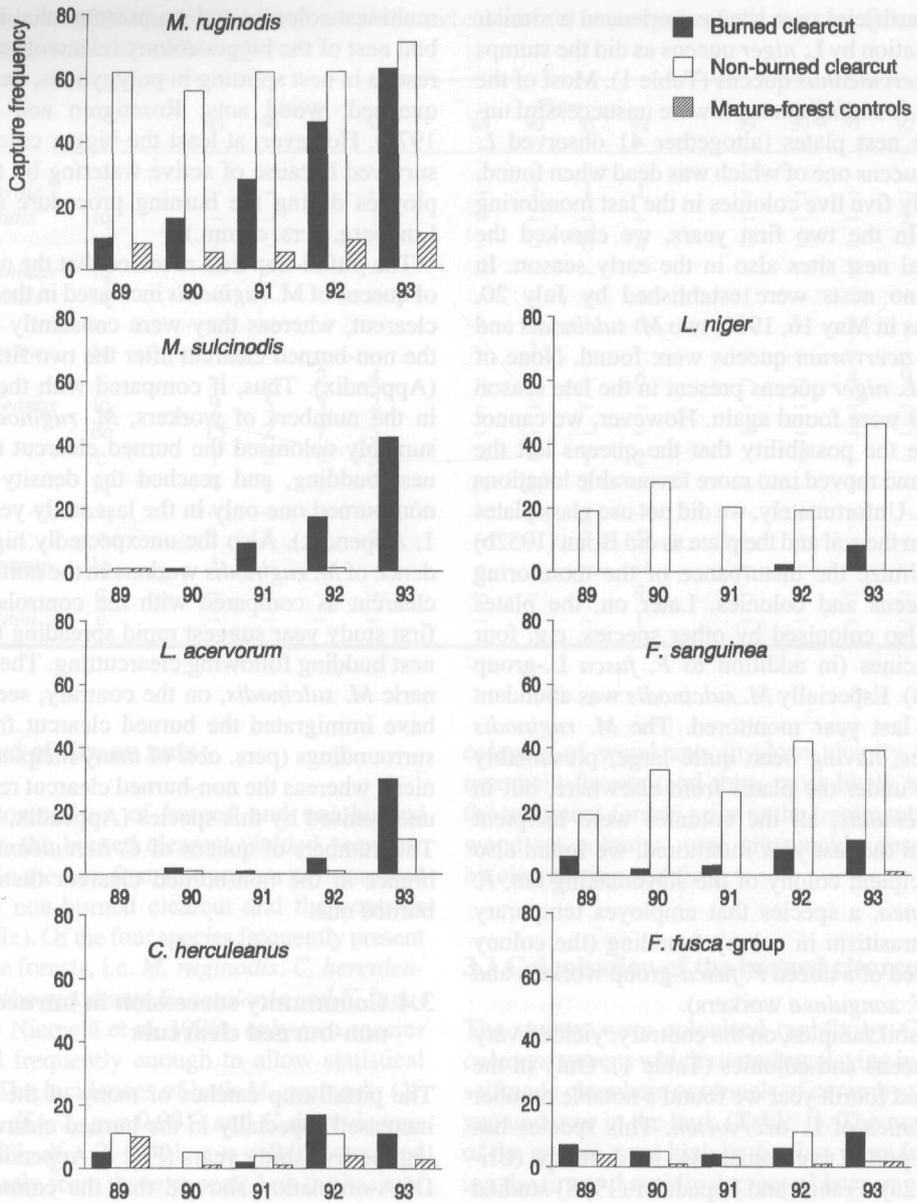


Fig. 1. The capture frequencies of common ants in the burned clearcut, non-burned clearcut, and mature-forest controls in 1989–1993 (two sampling periods pooled). Note that the sampling effort in the mature-forest controls was one fourth of that in the clearcuts (see Material and methods).

in all areas, and it increased in the burned clear-cut during the study, whereas the wood ants and *C. herculeanus* were more common in mature forests (Fig. 3).

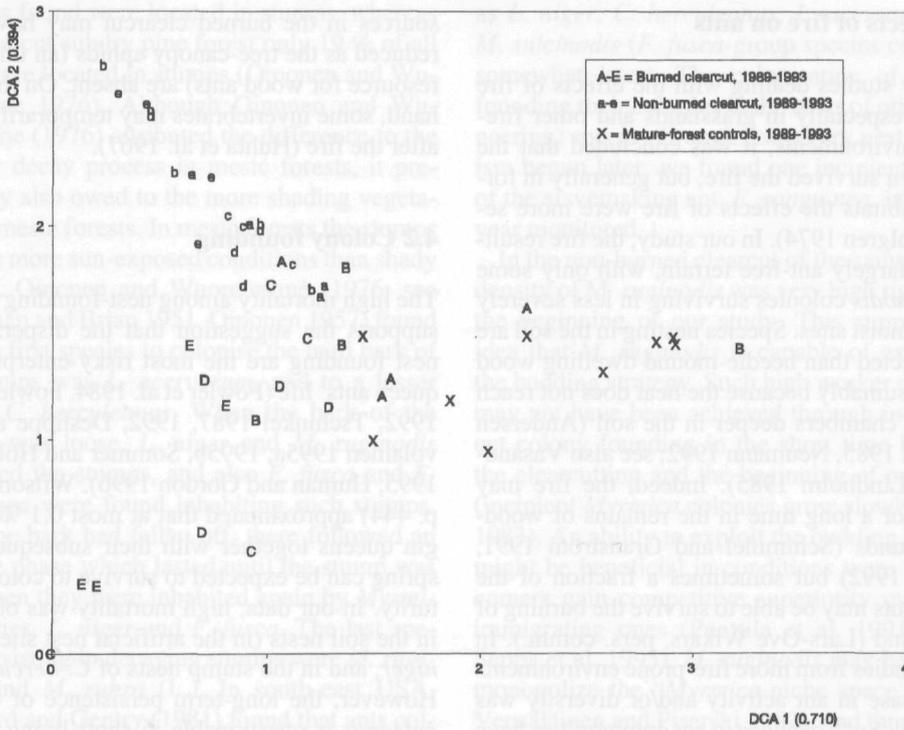


Fig. 2. DCA ordination of the sampling sites according to their ant samples. Key for symbols is given in the figure. Eigenvalues of the DCA axes are given in parentheses.

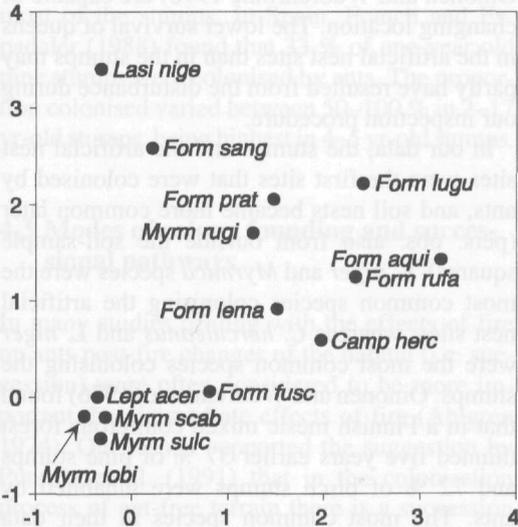


Fig. 3. DCA ordination of ant species in the sampling sites (parallel to Fig. 2). The point for *Myrmica lobicornis* is indicated by an arrow.

4 Discussion

Four main conclusions arise from our results: (1) Clearcutting and fire seemed to have resulted in destruction of the colonies of the old-growth dominants, the wood ants, but also other mature-forest species suffered in severely burned areas. (2) Independent colony founding was very risky for the ant queens because of the high mortality. (3) There seemed to be a succession of colony-founding modes in the ants supporting the suggestion of Punttila et al. (1991) that the first comers are capable of independent colony founding and that they are followed by species employing dependent strategies. (4) The communities in burned and non-burned clearcuts diverged from each other suggesting different successional pathways.

4.1 Effects of fire on ants

In many studies dealing with the effects of fire on ants especially in grasslands and other fire-prone environments, it was concluded that the ants often survived the fire, but generally in forested habitats the effects of fire were more severe (Ahlgren 1974). In our study, the fire resulted in a largely ant-free terrain, with only some *M. ruginodis* colonies surviving in less severely burned moist sites. Species nesting in the soil are less affected than needle-mound dwelling wood ants presumably because the heat does not reach the nest chambers deeper in the soil (Andersen and Yen 1985, Neumann 1992; see also Vasander and Lindholm 1985). Indeed, the fire may gloom for a long time in the remains of wood-and mounds (Schimmel and Granström 1991, Wikars 1992) but sometimes a fraction of the inhabitants may be able to survive the burning of the mound (Lars-Ove Wikars, pers. comm.). In many studies from more fire-prone environments an increase in ant activity and/or diversity was observed. Such changes in ant communities have been attributed to (1) changes in vegetation and habitat simplification (increased trappability on burned ground as compared with that in dense vegetation; Majer 1980, O'Dowd and Gill 1984, Andersen and Yen 1985, McCoy and Kaiser 1990, Andersen 1991, Neumann and Tolhurst 1991, York 1994), (2) changes in resource levels (reduced resources force the ants to forage further away from their colonies, or increased seed fall activates seed-harvesting species; Majer 1980, Andersen and Yen 1985, Andersen 1988, 1991, McCoy and Kaiser 1990, Neumann 1991, 1992, Neumann and Tolhurst 1991), and (3) direct and indirect competitive effects (competitive release when a superior competitor suffers disproportionately from the fire; Andersen and Yen 1985, Donnelly and Giliomee 1985, Andersen 1988, 1991, MacKay et al. 1991). In our data, the lower incidences of *M. ruginodis* and *C. herculeanus* in the burned clearcut than in the controls regardless of the simplification of the habitat and competitive release (destruction of wood-ant colonies) presumably implicate true colony mortality caused by fire. Indeed, such reduction in the numbers of *M. ruginodis* was not observed in the non-burned clearcut. The amount of re-

sources in the burned clearcut may have been reduced as the tree-canopy aphids (an important resource for wood ants) are absent. On the other hand, some invertebrates may temporarily boost after the fire (Huhta et al. 1967).

4.2 Colony founding

The high mortality among nest-founding queens supports the suggestion that the dispersal and nest founding are the most risky enterprises in queen ants' life (Fowler et al. 1984, Fowler 1987, 1992, Tschinkel 1987, 1992, Deslippe and Savolainen 1995a, 1995b, Sommer and Hölldobler 1995, Human and Gordon 1996). Wilson (1971, p. 444) approximated that at most 0.1 % of virgin queens together with their subsequent offspring can be expected to survive to colony maturity. In our data, high mortality was observed in the soil nests (in the artificial nest sites) of *L. niger*, and in the stump nests of *C. herculeanus*. However, the long-term persistence of *C. herculeanus* is questionable in short-living stumps (Sanders 1970). We cannot, however, attribute all the disappearances to queen mortality because the colonies of both *L. niger* (Oinonen 1956) and *M. ruginodis* (Brian and Brian 1951, Oinonen and Wuorenrinne 1976) are capable of changing location. The lower survival of queens in the artificial nest sites than in the stumps may partly have resulted from the disturbance during our inspection procedure.

In our data, the stumps and the artificial nest sites were the first sites that were colonised by ants, and soil nests became more common later (pers. obs. also from outside the soil-sample squares). *L. niger* and *Myrmica* species were the most common species colonising the artificial nest sites, whereas *C. herculeanus* and *L. niger* were the most common species colonising the stumps. Oinonen and Wuorenrinne (1976) found that in a Finnish mesic mixed coniferous forest thinned five years earlier 37 % of pine stumps and 72 % of birch stumps were inhabited by ants. The most common species in their data were *M. ruginodis* (92 of 159 nests encountered in 289 stumps) and *L. niger* (60 nests), whereas *C. herculeanus* inhabited only two pine stumps. In a clearcut mesic spruce forest 54 % of all ant

colonies found were located in stumps, whereas in a clearcut subdry pine forest only 19 % of all nests were located in stumps (Oinonen and Wuorenrinne 1976). Although Oinonen and Wuorenrinne (1976) attributed the difference to the quicker decay process in mesic forests, it presumably also owed to the more shading vegetation in mesic forests. In mesic forests the stumps provide more sun-exposed conditions than shady ground. Oinonen and Wuorenrinne (1976; see also Brian and Brian 1951, Oinonen 1957) found that the first species to colonise the hard bark of the stumps was *L. acervorum*, and to a lesser extent, *C. herculeanus*. When the bark of the stumps was loose, *L. niger* and *M. ruginodis* colonised the stumps, and also *F. fusca* and *F. sanguinea* were found inhabiting such stumps. After the bark had fallen off, there followed an ant-free phase which lasted until the stump was soft. Then they were inhabited again by *Myrmica* species, *L. niger* and *F. fusca*. The last species persisting in decaying stumps were *M. ruginodis* and *M. rubra* (L.). In south-east USA, Whitford and Gentry (1981) found that ants colonised snags only after they were channelized by termites. In Alberta, Wu and Wong (1987) found that 40 % of 4–29 yr-old lodgepole-pine stumps were colonised by ants. In their data, it took from 16 to 29 years before ants colonised most of the stumps. In Spain, Franch and Espadaler (1988) found that 33 % of one-year old pine stumps were colonised by ants. The proportion colonised varied between 50–100 % in 2–17 yr-old stumps, being highest in 4–5 yr-old stumps.

4.3 Modes of colony founding and successional pathways

In many studies dealing with the effects of fire on ants post-fire changes of the habitat (i.e. succession) were often considered to be more important than immediate effects of fire (Ahlgren 1974). Our results supported the suggestion by Punttila et al. (1991) that in the colonisation process of ant-free terrain there is a succession of immigrating species with different modes of colony founding. In our data, the first-coming pioneers in the burned clearcut were those that are capable of independent colony founding, such

as *L. niger*, *C. herculeanus*, *L. acervorum* and *M. sulcinodis* (*F. fusca*-group species colonised somewhat later). The colonisation of species founding their colonies in the nests of other (pioneering) species through temporary nest parasitism begun later: we found one incipient colony of the slavemaking ant, *F. sanguinea*, in the last year monitored.

In the non-burned clearcut of the same age the density of *M. ruginodis* was very high right from the beginning of our study. This supports the idea that *M. ruginodis* is capable of exploiting the budding strategy. Such high worker numbers may not have been achieved through independent colony founding in the short time between the clearcutting and the beginning of our study (incipient *Myrmica* colonies grow slowly; Brian 1983). An ability to exploit the budding strategy might be beneficial in conditions where the first comers gain competitive superiority over later immigrating ones (Punttila et al. 1991, 1994, Seppä et al. 1995). *M. ruginodis* may be able to monopolize the "Myrmica-niche space" (sensu Vepsäläinen and Pisarski 1982), and thus to prevent the colonisation of ecologically similar Myrmicines.

The ant-community succession of the burned clearcut differed from that of the non-burned one. The burned clearcut was characterized by the colonisation and growth of colonies of *M. sulcinodis*, steadily increasing numbers of *M. ruginodis*, and slightly higher numbers of *L. acervorum*. The non-burned clearcut, on the contrary, was densely inhabited by *M. ruginodis* already in the first study year, whereas *M. sulcinodis* did not colonise the area during our study. This presumably resulted from habitat differences between the two clearcuts, and possibly also from competition between *M. ruginodis* and *M. sulcinodis*. Ant queens seem to be capable of distinguishing suitable nesting habitats, e.g. disturbed areas, in flight for example on the basis of light reflection (Brian 1952a, Pontin 1960, Brian et al. 1966, Wilson and Hunt 1966, Fowler 1987, Tschinkel 1987). The non-burned clearcut was growing dense *Calamagrostis* and *Deschampsia* grasses already in the first study year and thus, the ground was presumably too shady and cool for *M. sulcinodis* (Elmes and Wardlaw 1982).

L. niger and *F. sanguinea* were present in the

non-burned clearcut already in the first study year, and their numbers increased in subsequent years. These aggressive species are rather strong competitors and they are well adapted to sun-exposed conditions. Thus, they are likely to prevent or slow down the colonisation of other aggressive species (Rosengren et al. 1979). Therefore, they are able to rule the community succession in a deterministic manner once they have established themselves in the area (Vepsäläinen and Pisarski 1982, Savolainen and Vepsäläinen 1988, Punttila et al. 1991, 1996, Punttila 1996). The slavemaking ant, *F. sanguinea*, seems to be one of the keystone species in open successional forest of the taiga. Punttila et al. (1996) suggested that ant communities in such forests are organized by direct and indirect effects of competition among the top competitors, the wood ants and the slavemaking ant. Oinonen (1956) found a similar kind of community divergence in open rocky forests. He suggested that competitive interactions resulted in distinct communities dominated either by *F. sanguinea* and *L. niger* or *F. fusca*. Similar community divergence has been found also in successional heathlands and sand-dune areas in Australia (Fox and Fox 1982, Fox et al. 1985, Majer 1985). Similarly, Andersen (1991) found that habitats with different fire regime hosted different ant communities, which was attributable to fire-induced habitat differences and competitive interactions. Our study area is characterized by a mosaic of young forest stands of various age, habitat type, and treatment history. This variation is reflected in differential colonisation by ants. The ant communities in young stands are shaped by various species interactions during succession resulting in a mosaic of distinct community types (Punttila et al. 1996, this study). The type of forest-management practice seems to be a key factor affecting the abundance and distribution of ant species. Thus this may have far-reaching consequences in forest ecosystems in the long run (Punttila et al. 1994).

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References

- Aarne, M. (ed.) 1995. Statistical yearbook of forestry 1995. Suomen virallinen tilasto. Maa- ja metsätalous, 1995:5, 354 p. The Finnish Forest Research Institute, Helsinki.
- Ahlgren, I. F. 1974. The effect of fire on soil organisms. In: Kozłowski, T. T. & Ahlgren, C. E. (eds), Fire and ecosystems, Academic Press, New York. p. 47–72.
- Andersen, A. N. 1988. Immediate and longer-term effects of fire on seed predation by ants in sclerophyllous vegetation in south-eastern Australia. *Australian Journal of Ecology* 13: 285–293.
- 1991. Responses of ground-foraging ant communities to three experimental fire regimes in a savanna forest of tropical Australia. *Biotropica* 23: 575–585.
- & Yen, A. L. 1985. Immediate effects of fire on ants in the semi-arid mallee region of northwestern Victoria. *Australian Journal of Ecology* 10: 25–30.
- Bentley, B. L. 1976. Plants bearing extrafloral nectaries and the associated ant community: interhabitat differences in the reduction of herbivore damage. *Ecology* 57: 815–820.
- Brian, M. V. 1952a. The structure of a dense natural ant population. *Journal of Animal Ecology* 21: 12–24.
- 1952b. Interaction between ant colonies at an artificial nest-site. *Entomologist's Monthly Magazine* 88: 84–88.
- 1983. Social insects. Ecology and behavioural biology. Chapman and Hall, London.
- & Brian A. D. 1951. Insolation and ant population in the west of Scotland. *Transactions of the Royal Entomological Society of London* 102: 303–330.

- , Hibble, J. & Kelly, A. F. 1966. The dispersion of ant species in a southern English heath. *Journal of Animal Ecology* 35: 281–290.
- Christensen, P. & Abbott, I. 1989. Impact of fire in the eucalypt forest ecosystem of southern Western Australia: a critical review. *Australian Forestry* 52: 103–121.
- Collingwood, C. A. 1979. The Formicidae (Hymenoptera) of Fennoscandia and Denmark. *Fauna Entomologica Scandinavica* 8: 1–174.
- Deslippe, R. J. & Savolainen, R. 1995a. Colony foundation and polygyny in the ant *Formica podzolica*. *Behavioral Ecology and Sociobiology* 37: 1–6.
- 1995b. Mechanisms of competition in a guild of formicine ants. *Oikos* 72: 67–73.
- Dlusskij, G. & Pisarski, B. 1971. Rewizja Polskich gatunków mrówek (Hymenoptera: Formicidae) z rodzaju *Formica* L. *Fragmenta Faunistica* (Warszawa) 16: 145–224.
- Donnelly, D. & Giliomee, J. H. 1985. Community structure of epigeaic ants (Hymenoptera: Formicidae) in fynbos vegetation in the Jonkershoek Valley. *Journal of the entomological Society of Southern Africa* 48: 247–257.
- Douwes, P. 1981. Hur man känner igen de olika arterna av den vanliga stackmyran. *Entomologisk Tidskrift* 102: 80–82. (In Swedish with an English summary.)
- Elmes, G. W. & Wardlaw, J. C. 1982. A population study of the ants *Myrmica sabuleti* and *Myrmica scabrinodis* living at two sites in the south of England. II Effect of above-nest vegetation. *Journal of Animal Ecology* 51: 665–680.
- Esseen, P.-A., Ehnström, B., Ericson, L. & Sjöberg, K. 1992. Boreal forests – the focal habitats of Fennoscandia. In: Hansson, L. (ed.), *Ecological Principles of Nature Conservation*, Elsevier, London. p. 252–325.
- Fowler, H. G. 1987. Colonization patterns of the leaf-cutting ant, *Atta bisphaerica* Forel: evidence for population regulation. *Journal of Applied Entomology* 104: 102–105.
- 1992. Patterns of colonization and incipient nest survival in *Acromyrmex niger* and *Acromyrmex balzani* (Hymenoptera: Formicidae). *Insectes Sociaux* 39: 347–350.
- , Robinson, S. W. & Diehl, J. 1984. Effect of mature colony density on colonization and initial colony survivorship in *Atta capiguara*, a leaf-cutting ant. *Biotropica* 16: 51–54.
- Fox, M. D. & Fox, B. J. 1982. Evidence for interspecific competition influencing ant species diversity in a regenerating heathland. In: Buckley, R. C. (ed.), *Ant-plant interactions in Australia*, Dr. W. Junk Publishers, The Hague. p. 99–110.
- Fox, B. J., Fox, M. D. & Archer, E. 1985. Experimental confirmation of competition between two dominant species of *Iridomyrmex* (Hymenoptera: Formicidae). *Australian Journal of Ecology* 10: 105–110.
- Franch, J. & Espadaler, X. 1988. Ants as colonizing agents of pine stumps in San Juan de la Pena (Huesca, Spain). *Vie Milieu* 38: 149–154.
- Haila, Y. 1994. Preserving ecological diversity in boreal forest: ecological background, research, and management. *Annales Zoologici Fennici* 31: 203–217.
- , Hanski, I. K., Niemelä, J., Puntila, P., Raivio, S. & Tukia, H. 1994. Forestry and the boreal fauna: matching management with natural forest dynamics. *Annales Zoologici Fennici* 31: 187–202.
- Hansen, A. J., Spies, T. A., Swanson, F. J. & Ohmann, J. L. 1991. Conserving biodiversity in managed forest. Lessons from natural forests. *BioScience* 41: 382–392.
- Hansson, L. (ed.) 1992. *Ecological principles of nature conservation*. Elsevier, London. 438 p.
- Heliövaara, K. & Väisänen, R. 1982. Effects of modern forestry on northwestern European forest invertebrates: a synthesis. *Acta Forestalia Fennici* 189: 1–32.
- Heyward, F. & Tissot, A. N. 1936. Some changes in the soil fauna associated with forest fires in the longleaf pine region. *Ecology* 17: 659–666.
- Huhta, V., Karpinen, E., Nurminen, M. & Valpas, A. 1967. Effect of silvicultural practices upon arthropod, annelid and nematode populations in coniferous forest soil. *Annales Zoologici Fennici* 4: 87–143.
- Human, K. G. & Gordon, D. M. 1996. Exploitation and interference competition between the invasive Argentine ant, *Linepithema humile*, and native ant species. *Oecologia* 105: 405–412.
- Kaila, L., Martikainen, P. & Puntila, P. 1996. Dead trees left in clearcuts benefit saproxylic Coleoptera adapted to natural disturbances in boreal forests. *Biodiversity and Conservation* (In press).
- Lyon, L. J., Crawford, H. S., Czuhai, E., Fredriksen, R. L., Harlow, R. F., Metz, L. J. & Pearson, H. A. 1978. Effects of fire on fauna: A state-of-knowledge review. U.S. Department of Agriculture, Forest Service, General Technical Report WO-6.

- MacKay, W.P., Rebeles, A. M., Arredondo, H. C. B., Rodriguez, A. D. R., Gonzalez, D. A. & Vinson, S. B. 1991. Impact of the slashing and burning of a tropical rain forest on the native ant fauna (Hymenoptera: Formicidae). *Sociobiology* 18: 257–268.
- Majer, J. D. 1980. Report on a study of invertebrates in relation to Kojonup Nature Reserve fire management plan. WAIT Department of Biology Bulletin number 2.
- 1985. Recolonization by ants of rehabilitated mineral sand mines on North Stradbroke Island, Queensland, with particular reference to seed removal. *Australian Journal of Ecology* 10: 31–48.
- McCoy, E. D. & Kaiser, B. W. 1990. Changes in foraging activity of the southern harvester ant *Pogonomyrmex badius* (Latreille) in response to fire. *American Midland Naturalist* 123: 112–123.
- Morais, de H. C. & Benson, W. W. 1988. Recolonization of cerrado vegetation by arboricolous ants after fire. *Revista Brasileira de Biologia* 48: 459–466. (In Portuguese with an English summary).
- Muona, J. & Rutanen, I. 1994. The short-term impact of fire on the beetle fauna in boreal coniferous forest. *Annales Zoologici Fennici* 31: 109–121.
- Neumann, F. G. 1991. Responses of litter arthropods to major natural or artificial ecological disturbances in mountain ash forest. *Australian Journal of Ecology* 16: 19–32.
- 1992. Responses of foraging ant populations to high-intensity wildfire, salvage logging and natural regeneration processes in *Eucalyptus regnans* regrowth forest of the Victorian Central Highlands. *Australian Forestry* 55: 29–38.
- & Tolhurst, K. 1991. Effects of fuel reduction burning on epigeal arthropods and earthworms in dry sclerophyll eucalypt forest of west-central Victoria. *Australian Journal of Ecology* 16: 315–330.
- Niemelä, J., Haila, Y. & Punttila, P. 1996. The importance of small-scale heterogeneity in boreal forests: variation in diversity in forest-floor invertebrates across the succession gradient. *Ecography* 19: 352–368.
- O'Dowd, D. J. & Gill, A. M. 1984. Predator satiation and site alteration following fire: mass reproduction of alpine ash (*Eucalyptus delegatensis*) in south-eastern Australia. *Ecology* 65: 1052–1066.
- Oinonen, E. A. 1956. On the ants of the rocks and their contribution to the afforestation of rocks in southern Finland. *Acta Entomologica Fennica* 12: 1–212. (In Finnish with an English summary).
- 1957. Wood as nest base for ants. Reprint from *Metsätietoa* 1/1957, Helsinki. 4 pp. (In Finnish with an English summary).
- & Wuorenrinne, H. 1976. Über die finnischen Ameisenarten aus waldpflegerischen Gesichtspunkten. *Waldhygiene* 11: 167–170.
- Paine, R. T. 1995. A conversation on refining the concept of keystone species. *Conservation biology* 9: 962–964.
- Pearse, A. S. 1943. Effects of burning-over and raking-off litter on certain soil animals in the Duke forest. *American Midland Naturalist* 29: 406–424.
- Pontin, A. J. 1960. Field experiments on colony foundation by *Lasius niger* (L.) and *L. flavus* (F.). *Insectes Sociaux* 7: 227–230.
- Punttila, P. 1996. Succession, forest fragmentation, and the distribution of wood ants. *Oikos* 75: 291–298.
- , Haila, Y., Niemelä, J. & Pajunen, T. 1994. Ant communities in fragments of old-growth taiga and managed surroundings. *Annales Zoologici Fennici* 31: 131–144.
- , Haila, Y., Pajunen, T. & Tukia, H. 1991. Colonisation of clearcut forests by ants in southern Finland: a quantitative survey. *Oikos* 61: 250–262.
- , Haila, Y. & Tukia, H. 1996. Ant communities in clearcut southern Finnish taiga forests: habitat effects and species interactions. *Ecography* 19: 16–28.
- Rassi, P. & Väisänen, R. (eds.) 1987. Threatened animals and plants in Finland. English summary of the report of the Committee for the Conservation of Threatened Animals and Plants in Finland. Ministry of the Environment, Helsinki. 82 p.
- Rosengren, R. & Pamilo, P. 1978. Effect of winter timber felling on behaviour of foraging wood ants (*Formica rufa*-group) in early spring. *Memorabilia Zoologica* 29: 143–155.
- , Vepsäläinen, K. & Wuorenrinne, H. 1979. Distribution, nest densities, and ecological significance of wood ants (the *Formica rufa*-group) in Finland. *O.I.L.B. Bull. SROP*, II, 3: 181–213.
- Sanders, C. J. 1970. The distribution of carpenter ant colonies in the spruce-fir forests of northwestern Ontario. *Ecology* 51: 865–873.
- Savolainen, R. & Vepsäläinen, K. 1988. A competition hierarchy among boreal ants: impact on resource partitioning and community structure. *Oikos* 51: 135–155.

- Schimmel, J. & Granström, A. 1991. Skogsbränderna och vegetationen. Skog och Forskning 4:39–46. (In Swedish).
- Seppä, P., Sundström, L. & Punntila, P. 1995. Facultative polygyny and habitat succession in boreal ants. *Biological Journal of the Linnean Society* 56: 533–551.
- Sommer, K. & Hölldobler, B. 1995. Colony founding by queen association and determinants of reduction queen number in the ant *Lasius niger*. *Animal Behaviour* 50: 287–294.
- Ter Braak, C. J. F. 1987. CANOCO – A FORTRAN program for canonical community ordination by partial detrended canonical correspondence analysis, principal component analysis and redundancy analysis. TNO Institute of Applied Computer Science. Wageningen. The Netherlands. 95 p.
- Tschinkel, W. R. 1987. The fire ant, *Solenopsis invicta*, as a successful “weed”. In: Eder, J. & Rembold, H. (eds), *Chemistry and biology of social insects*, Verlag J. Peperny, Munich. p. 585–588.
- 1992. Brood raiding and the population dynamics of founding and incipient colonies of the fire ant, *Solenopsis invicta*. *Ecological Entomology* 17: 179–188.
- Vasander, H. & Lindholm, T. 1985. Fire intensities and surface temperatures during prescribed burning. *Silva Fennica* 19: 1–15.
- Vepsäläinen, K. & Pisarski, B. 1982. Assembly of island ant communities. *Annales Zoologici Fennici* 19: 327–335.
- Warren, S. D., Scifres, C. J. & Teel, P. D. 1987. Response of grassland arthropods to burning: a review. *Agriculture, Ecosystems and Environment* 19: 105–130.
- Whitford, W. G. & Gentry, J. B. 1981. Ant communities of southeastern longleaf pine plantations. *Environmental Entomology* 10: 183–185.
- Wikars, L.-O. 1992. Skogsbränder och insekter. *Entomologisk Tidskrift* 113:1–11. (In Swedish with an English summary).
- 1995. Clear-cutting before burning prevents establishment of the fire-adapted *Agonum quadripunctatum* (Coleoptera: Carabidae). *Annales Zoologici Fennici* 32: 375–384.
- Wilson, E. O. 1971. *The insect societies*. Belknap Press of Harvard University, Cambridge, Mass. 548 p.
- & Hunt, G. L. Jr. 1966. Habitat selection by the queens of two field dwelling species of ants. *Ecology* 47:485–487.
- Wu, J. & Wong, H. R. 1987. Colonization of lodgepole pine stumps by ants (Hymenoptera: Formicidae). *The Canadian Entomologist* 119: 397–398.
- York, A. 1994. The long-term effects of fire on forest ant communities: management implications for the conservation of biodiversity. *Memoirs of the Queensland Museum* 36: 231–239.
- Zackrisson, O. 1977. Influence of forest fires on the North Swedish boreal forest. *Oikos* 29: 22–32.

Total of 79 references

Appendix. Total samples (w) and occurrence frequencies (f) of worker ants, and total samples of queen ants (q) in the pitfall-trap data from burned and non-burned clearcuts (total = 2 periods × 52 traps in each) and mature-forest controls (total = 2 periods × 26 traps, 13 traps in two forests) in 1989–1993.

Species	Burned clearcut			Non-burned clearcut			Controls			Total	
	89	90	91	92	93	89	90	91	92		93
<i>Myrmica lobicornis</i> Nylander											
w					2						2
f					2						2
q			1	1	2						9
<i>Myrmica ruginodis</i> Nylander											
w	11	33	71	134	270	133	162	222	178	203	1464
f	10	16	28	46	63	62	56	62	62	71	514
q		7	5	4	22	3	11	40	42	45	184
<i>Myrmica scabrinodis</i> Nylander											
w					4						4
f					3						3
q										3	3
<i>Myrmica sulcinodis</i> Nylander											
w		2	12	24	114	1					5
f		1	9	17	42	1					156
q											72
<i>Leptothorax acervorum</i> (Fabricius)											
w		2	1	5	48						2
f		2	1	5	30						78
q	2					1					51
<i>Camponotus herculeanus</i> (Linné)											
w	5		2	25	13	11	5	4	14		9
f	5		2	17	11	11	5	4	11		102
q	1	1				14	7	1	2		85
<i>Lasius niger</i> (Linné)											
w				4	10	34	88	47	139	244	26
f				2	8	19	28	20	19	46	566
q						1					142
<i>Lasius fuliginosus</i> (Latreille)											
w			3	4	11						2
f			3	4	9						29
q											25
<i>Formica fusca</i> Linné											
w	7	5	1	2	2	7	9	4	6	1	1
f	7	5	1	2	2	5	5	3	6	6	49
<i>Formica lemni</i> Bondroit											
w											2
f											2

<i>Formica exsecta</i> Nylander	q	1	41	207	193	934	313	1	1	1739
<i>Formica sanguinea</i> Latreille	w	29	19	33	26	42	39	1	1	190
	f	11	3	2	-	-	-	-	-	12
<i>Formica rufa</i> Linné	q	2	-	-	-	-	-	-	-	3
	w	-	-	-	-	-	-	-	-	3
	f	-	-	-	-	-	-	-	-	3
<i>Formica aquilonia</i> Yarow	w	-	3	1	-	-	-	-	-	8442
	f	-	3	1	-	-	-	-	-	141
<i>Formica lugubris</i> Zetterstedt	q	-	2	-	-	2	-	-	5	16
	w	-	1	-	-	3	1	-	1	12
	f	-	1	-	-	3	1	-	1	11
<i>Formica pratensis</i> Retzius	q	-	5	-	-	-	-	-	1	11
	w	-	1	-	-	-	-	-	-	1
	f	-	1	-	-	-	-	-	-	1
Total	w	503	232	474	470	1284	783	588	721	12647
Total	w	27	29	23	42	50	52	4	2	278
	q	7	40	49	94	10	7	7	1988	4912
	f	7	13	10	7	27	7	2	1977	4891
	w	7	4	4	1	1	2	21	26	26
	f	5	4	4	1	1	1	3	21	26
	q	3	1	1	1	2	-	-	-	5
	w	3	1	1	1	3	1	1	1	1
	f	2	1	1	1	3	1	1	1	1
	q	1	3	1	1	5	-	-	1	11
	w	1	-	-	-	-	-	-	-	1
	f	1	-	-	-	-	-	-	-	1

Site Index Curves for European Aspen (*Populus tremula* L.) Growing on Forest Soils of Different Soils in Sweden

Tord Johansson

Site index curves for European aspen (*Populus tremula* L.) growing on forest soils of different soil types in Sweden. *Silva Fennica* 30(4): 437-451.

Site index curves for European aspen (*Populus tremula* L.) stands in Sweden. The stands ranged in latitude from 56 to 60°N, were 22 years (range 12-63), the mean stand density 1075 (41), and the mean diameter at breast height (on back) 13 cm.

Site index curves for total age. Curves for H_{10} (stem height at 10 m) for total age. Curves fitted for H_{10} total age have been compared by other Nordic studies. The curves from the present study are steeper than curves from norwegan and 20-year old aspen stands, curves from the present study are steeper than curves from the present study.

The stands were grouped into three groups: sandy till (17), clay till (4), A; there was only one stand growing in the fine till in the heavy clay till group and two stands in the silty till group. The curves were fitted with growth curves. There were no statistically significant differences between the three soil type groups.

The importance of aspen stand age given. Damage caused by insects are also used as a problem for height yield productivity.

Populus tremula L., site index curves, total age, soil type.

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