Ann. Zool. Fennici 31:109–121
Helsinki 31 January 1994
ISSN 0003-455X

The short-term impact of fire on the beetle fauna in boreal coniferous forest

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Received 18 August 1993, accepted 1 November 1993

The immediate changes caused by forest fire in the beetle fauna were studied at three sites in boreal coniferous forest in Finland. In general the number of individuals and species increased after fire. The species attracted to the burnt forest included wood-borers (Cerambycidae, Curculionidae, Anobiidae, some Elateridae), species developing under bark of damaged trees, species associated with fungi (Lathrididae, Cryptophagidae, Nitidulidae, Leiodidae) and certain soil- and litter-dwelling groups: Carabidae, Byrrhidae and some Elateridae. Predators utilizing diptera larvae in mushrooms increased strongly after the fire as well. Many of the species presumed to be associated with wood-fungi peaked immediately after the fire, i.e. many cryptophagids, lathridids and nitidulids, whereas the leiodids *Anisotoma* spp. and *Agathidium* spp. became commoner two years after the fire. Several species previously known to strongly prefer burnt forests were captured. The fire specialists form a hetergenous ecological group, indicating that a substantial portion of the forest species have adapted to fire cycles. A large group of species normally found only in man-made, microclimatically warm habitats, e.g. compost, were attracted to two of the burnt sites. Their absence from the third site was probably due to lack of suitable source areas in the immediate surroundings. Cholevidae associated with rodents and many litter-dwelling Staphylinidae were drastically reduced by the fire. In most cases, their numbers had not returned to previous levels two years after the burning.

1. Introduction

Our knowledge of the extent, frequency and impact of forest fires is fairly modest (Zackrisson 1977, Hyvärinen & Sepponen 1988). Very little is known about the impact of fires on beetles, although we do know that some species appear to require fires and others seem to favour areas affected by them (e. g. Palm 1951, 1959, Lundberg 1984, 1993, Holliday 1984, 1991, Wikars

1992, Ahnlund & Lindhe 1992). There are indications that the effect of forest fires on the insect fauna can be detected decades later (Wikars & Ås 1991). These questions have extensive practical implications, as a fair number of the species included in the Finnish Red List are somehow dependent on forest fires (Rassi & al. 1986, 1992). No doubt this holds for much of Western and Central Europe as well, although competently compiled lists of threatened species are not available from most areas.

Our aim is to describe the preliminary results of three burning experiments made in Finland. Because of the practical problems involved, we could not obtain sufficient data for statistical testing. Nevertheless, we choose to describe trends observed in the material even though we fully realize that some may turn out to be artefacts.

2. Material and methods

2.1. Study sites

All the three areas studied were part of the western fringe of the Siberian taiga forest in Eastern Finland.

Site 1

Kuusamo, Uudenniitynlampi (Grid 27°E 7374: 606).

The Kuusamo site was located within the northern boreal zone (Abrahamsen et al. 1977). The forest belonged to the *Empetrum-Myrtillus* type (EMT, Cajander 1949), with the dominant tree species being Norway spruce aged about 200 years. Other species, especially Scots pine and birch, were present in small numbers. The site, about 5 hectares in size, was one of many forest islands in a fairly extensive bog and thus somewhat isolated from continuous forested areas. Limited selective logging had occurred at this site more than 40 years before the experiment. Both fallen and standing dead trees were present in fair numbers, most of them being spruce. Unless carefully assessed, the forest appeared to be unmanaged, "primeval".

Site 2

Pohjois-Karjala, Patvinsuo, Lahnasuo (Grid 27°E 7007:682).

This site was located within the south boreal zone (Abrahamsen et al. 1977). The forest belonged to the *Calluna* type (CT, Cajander 1949), the dominant tree species being Scots pine aged about 90 years. Norway spruce was present in the NE corner, where also numerous wind-fallen, dead trunks of spruce could be found. A few scattered birches were present as well. The site, 1.1 hectares in size, was one of many forest islands in an extensive bog and thus somewhat isolated from continuous forested areas. A few standing dead trees were present, most of them being pines. This forest also appeared to be unmanaged, "primeval".

Site 3

Karjala, Patvinsuo, Surkansuo (Grid 27°E 7010: 685).

This site was similarly situated as site 2 and 1.1 hectares in size. It had been logged, and the dominant pines were now only about 40 years old. There were, however, some old pines at the center of the forest island.

2.2. Burning of the sites

An attempt was made to burn site 1 in the spring of 1991, but because of unfavourable weather this plan had to be aborted. Nearly no changes to the vegetation could be observed after this unsuccessful try. The forest was properly burnt in late May, 1992. The ground layer was completely destroyed and many spruces perished, but the fire was not fierce enough to kill pine trees. Only the western half of the site was burnt; the eastern half was left untouched.

Both sites 2 and 3 were burned in June 26–27. 1989, the ground layer burnt nearly completely and at least the younger spruces in site 2 perishing. Most of the pines were not killed, but many trunks were damaged by the fire. Most of the barkless burnt pine snags were brought down.

2.3. Collecting and sampling of the beetles

The number of traps, dates and trap days from all sites are given in Table 1.

Site 1. Ten sets of traps were placed at the study site. Five sets were placed both at the site to be burnt and in similar forest next to it. Every set included two window flight traps (WT) and four pitfall traps (PT). The PTs were placed in a line about two meters apart and the WTs were placed at the two ends of the line, about 1 meter high, hanging from the nearest available trees. The PTs had a diameter of 75 mm and a depth of 150 mm. The WTs were of the type shown in Fig. 1A. All traps contained 5% ethylenglycol solution with a small amount of detergent. Background collecting was done in 1990. Although the first burning attempt failed nearly completely in 1991, the material collected during that year was omitted; it would have been very difficult to evaluate the impact of the aborted try.

Site 2. Three sets of window traps were placed at different localities on the burnt area. Every set included two window traps of the type shown in Fig. 1B. In summer 1990 five additional window traps of the type shown in Fig. 1A were used in site 2. Twenty pitfall traps, 65 mm wide and 85 mm deep, were placed across the burnt area in two rows about 30 metres apart, while in each row the traps set about five meters from each other. All the traps contained a saturated NaCl solution with a small amount of detergent added. Background collecting was done in 1987 and 1988.

Site 3. One set of two window traps (Fig. 1B) was placed at the center of the burnt area, and two rows of ten pitfall traps were placed as in site 2. Background collecting was done in 1988, but no WTs were used at that time.

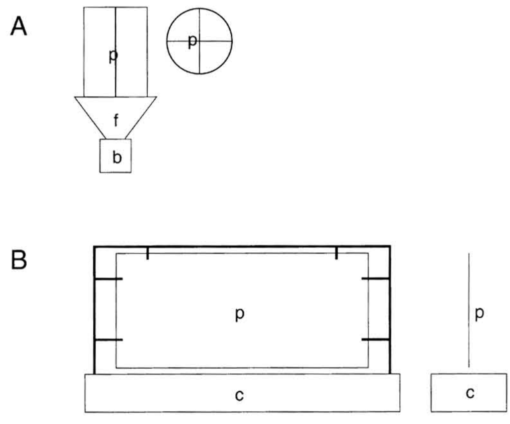

Fig. 1. Two types of window flight traps (height ca. 50 cm). — A. Cylindrical, seen from the side and from above. b = changeable container with trapping fluid; f = funnel; p = transparent plastic plates. — B. Rectangular, seen from the front and from the side. c = collecting container with trapping fluid; p = transparent plastic plates.

Table 1. Number of traps, trapping periods and trap days at the study sites. W = window flight traps, P = pitfall traps.

	Year	Number of traps (W/P)	Trapping period	Days	Trap days (W/P)
Site 1, Kuusamo, before burning	1990	20/40	20.6.–4.10.	105	2100/4200
Site 1, Kuusamo, untouched part	1992	10/20	30.5–26.9.	105	1050/2100
Site 1, Kuusamo, burnt part	1992	1020	30.5.–26.9.	105	1050/2100
Site 2, Karjala, before burning	1987–1988	6/20	20.7.–30.8. & 7.6.–30.7.	96	576/1920
Site 2, Karjala, after burning	1989	6/20	29.6.–6.9.	70	420/1200
	1990	11/20	24.5.–18.9.	118	1298/2320
	1991	6/20	22.5.–14.9.	116	696/2320
Site 3, Karjala, before burning	1988	–/20	7.6.–30.7.	53	–/1060
Site 3, Karjala, after burning	1989	2/20	29.6.–6.9.	70	140/1400
	1990	2/20	24.5.–18.9.	118	236/2360
	1991	2/20	22.5–14.9.	116	232/2320

3. Results and discussion

3.1. Number of species and specimens caught

The sample from site 1 included 111 species and 1263 exx. before burning, 138 species and 1771 exx. after half of the site was burnt. At site 2 we obtained 227 species and 1986 exx. before burning and 479 species and 9058 exx. after it. The corresponding values for site 3 are 88 species and 530 exx. and 258 species and 3094 exx, respectively. The numbers of all abundant species caught are given in Tables 2 and 3. These tables include all known fire-loving species as well as species dependent upon man-made agricultural habitats — even though caught in lesser numbers. The systematic position of the genera listed in Tables 2–4 appears in the appendix. The changes between yearly catches after the fire at sites 2 and 3 are given for the commonest species in Table 4. The nomenclature follows Silfverberg 1992.

A complete list of the species caught is available from the authors and will be published in a National Board for Waters and Enviroment Bulletin.

When comparing beetle catches between separate years it is extremely difficult to evaluate the impact of an unexpected catastrophe like a fire. Very little is known about the normal yearly variation in beetle populations other than the carabids. The data available suggest that at least in the Finnish coniferous forests the yearly variation in the abundance of species can be 6- to 10-fold, with the fluctuation in numbers of specimens varying strongly and independently within different species (Muona, unpublished). In addition, most existing data have been collected with pitfall traps. It has been shown that the correlation between locomotive activity and the "true" density of soil-dwelling beetles varies between species (Greenslade 1964a, 1964b, Desender & Maelfait 1986, Halsall & Wratten 1988, Assing 1993, Siitonen pers. comm., Muona, unpublished). It is reasonable to expect the locomotive activity of a species to vary depending on its reproductive stage, its sex, and the abiotic features of the site. Unless large samples covering the whole growing season are available, yearly catches are very difficult to compare reliably. In actual fact, the sampling period should cover the whole year even in boreal regions like Scandinavia. The most numerous and absolutely dominant soil-dwelling beetle in dry pine forests in the Kuusamo region in Finland, the staphylinid *Oxypoda islandica* Kr., emerges at the time of the first snowfall in autumn and in winter can be caught in large numbers only underneath the permanent snow-cover (Muona, unpublished).

For practical reasons we were not able to collect through the whole growing season, and the variation in weather conditions was extensive between the years 1987 and 1991. These features in combination with the problems stemming from the trapping methods available suggest that the data at our disposal should be used only in a search for general trends. More exact analysis would require extensive background information not yet available. We have adopted the view that identical changes observed in at least two burnt sites suggest features typical to burnt coniferous forest in the boreal zone. If changes were observed at one site only, the reasons are given why we might consider this as not directly connected with the fire.

3.2. Fire specialists

At site 1 three fire specialists were observed the summer after the fire: *Amara nigricornis*, *Henoticus serratus* and *Cryptophagus corticinus*, whereas two additional ones, *Hylobius abietis* and *H. pinastri*, increased in number. At sites 2 and 3, several species known to favour recently burnt forests were found after the treatment: *Sericoda quadripunctata*, *Micropeplus tesserula*, *Paranopleta inhabilis*, *Sphaeriestes stockmanni*, *Cryptophagus corticinus*, *Laemophloeus muticus*, *Pediacus fuscus*, *Stephanopachys substriatus*, *Acmaeops marginata* and *Platyrhinus resinosus*. Two additional ones increased in numbers: *Caenoscelis ferruginea* and *Hylobius abietis*. The most frequently collected fire-specialists were *P. fuscus*, *C. ferruginea* and *H. abietis*, which all showed slightly different patterns after the fire. *P. fuscus* and *H. abietis* peaked the same year the forest was burnt, *H. abietis* being fairly abundant even the year after, whereas *C. ferruginea* showed a more modest, slow and continuous increase.

Table 2. Site 1, Kuusamo, pitfall (PF) and window trap (WT) catches before and after the burning, number of specimens per 1000 trapping days. Species found in excess of 10 exx. included, plus all known strict fire-specialists (**). U = untouched part of area, B = burnt part of area.

	PF			WT		
	Before	U after	B after	Before	U after	B after
Ground-layer predators						
Bembidion grapii Gyll.	0	0.95	3.33	0.48	0	0
Pterostichus adstrictus Esch.	0.24	0.95	4.76	0	0	0
Calathus micropterus (Duft.)	15.95	9.52	37.14	0	0	0
***Amara nigricornis* Thoms.	0	0	2.86	0	0	0
Agabus congener (Thunb.)	0.71	0.95	1.92	0	0	0
Arpedium quadrum (Grav.)	13.57	4.76	0	0.96	0	0.96
Coryphium angusticolle Steph.	3.09	9.52	3.33	8.57	4.76	5.71
Mycetoporus lepidus (Grav.)	0.48	0	3.33	0	0	0
Ischnosoma splendidum (Grav.)	0.95	5.24	3.33	0	0	0
Liogluta micans (Muls. & Rey)	6.90	1.90	0.48	0	0	0
Atheta aeneipennis (Thoms.)	4.76	1.90	3.80	0	0	0
Lypoglossa lateralis (Mann.)	0.24	0	4.76	0	0.96	1.92
Zyras humeralis (Grav.)	29.76	143.80	16.67	0	0	0
Ground-layer non-predators						
Byrrhidae	0.72	0.48	22.37	0	0	0
Species developing deep in soil						
Soil-dwelling Elateridae	0.48	0.48	4.29	0	4.76	1.90
Species associated with rodents						
Sciodrepoides watsoni (Spence)	2.14	0.48	0.48	0	0	0
Catops nigrita Er.	29.28	18.09	0	0.96	0.96	0
Species specializing in temporary resources						
Deliphrum tectum (Payk.)	13.57	14.29	19.05	0	0	7.62
Tachinus pallipes (Grav.)	4.29	5.71	15.71	0.48	1.92	5.71
Loridthon thoracicus (F.)	0.95	2.85	4.23	0	0	0
Atheta lapponica J. Sahlb.	0	0	3.33	0	0	2.86
Predators living under tree-barks						
Nitidulidae	0	0.96	0	0.48	4.76	14.29
Rabocerus foveolatus (Ljungh)	0	0	0	0.48	1.92	15.24
Species developing in wood attacked by fungi						
Wood-boring Elateridae	0.48	1.92	1.92	0	0	0
Species attracted to damaged and dead trees						
***Henoticus serratus* (Gyll.)	0	0	0	0	0	0.95
***Cryptophagus corticinus* Thoms.	0	0	0	0	0	0.95
"All cryptophagids"	0.48	1.44	4.76	2.38	5.71	35.23
Latridiidae	0	0	0.96	0.96	1.92	19.05
Pogonocherus fasciculatus (Deg.)	0.24	0.48	2.86	0.48	0	1.90
***Hylobius abietis* (L.)	1.14	8.57	48.09	0	23.81	1.90
***H. pinastri* (Gyll.)	1.14	0.96	8.57	0.48	0	0
Pissodes pini (L.)	0	0.48	9.05	0.48	0	1.92
Hylurgops palliatus (Gyll.)	0.48	0	0	0	7.62	0.95
Hylastes brunneus Er.	0.71	0	0	0	38.09	9.50
Hylastes cunicularius Er.	1.67	1.44	7.62	5.24	1.90	5.71
Polygraphus punctifrons Thoms.	0	0	0	0	2.86	12.38
Pityogenes chalcographus (L.)	0.24	0	3.33	0	7.62	6.67
Dryocoetes autographus (Ratz.)	0.24	0.48	0.48	2.38	7.62	7.62
Trypodendron lineatum (Ol.)	0	0	0	0.48	7.62	6.67
"All scolytids"	4.76	1.90	12.86	9.52	95.24	67.62
Herbivores						
Otiorhynchus nodosus (Muller)	1.43	0.48	5.95	0	0	0
Predators living on vegetation						
Anthophagus omalinus Zett.	4.29	3.81	0	2.86	0	0
Scirtidae	6.90	5.71	2.86	30.95	33.33	7.62
Cantharidae	0.95	4.76	1.43	22.38	40.95	32.38
Anaspidae	0.24	2.38	1.90	31.43	42.86	12.38

Table 3. Sites 2 and 3, Pohjois-Karjala. Pitfall (PF) and window trap (WT) catches before (B) and after (A) burning, number of specimens per 1000 trapping days. Species found in excess of 20 exx. are included, plus all known strict fire-specialists (**) and species associated with agriculture.

	Site 2				Site 3		
	PF-B	PF-A	WT-B	WT-A	PF-B	PF-A	WT-A
Ground-layer predators							
Notiophilus germinyi Fauvel	0.52	0.82	0	0	0.94	3.53	0
N. biguttatus (F.)	0	2.30	0	0	0	1.32	0
Miscodera arctica (Payk.)	0	1.47	0	0	0	2.96	0
Patrobus assimilis Chaud.	0	2.79	0	0	0	0.49	0
Bembidion grapii Gyll.	0	8.38	0	0.41	0	1.64	0
Pterostichus adstrictus Esch.	0	12.00	0	0.41	0	6.56	0
P. oblongopunctatus (F.)	0.52	2.30	0	0	0.94	0.98	0
P. rhaeticus Heer	2.08	1.48	0	0	9.40	2.47	0
Calathus micropterus (Duft.)	9.38	39.80	0	0.41	35.85	56.25	0
Agonum fuliginosum (Panz.)	2.60	5.43	0	0	3.77	0	0
Gabrius trossulus (Nordm.)	0	0.16	0	11.20	0	0	1.64
Xantholinus tricolor (F.)	0	0	0	0	4.72	5.76	0
Acidota crenata (F.)	0	7.29	0	0.49	0	4.44	3.28
Mycetoporus lepidus (Grav.)	3.65	8.55	3.47	34.44	0.94	8.06	37.83
Ischnosoma splendidum (Grav.)	7.29	3.45	0	0	16.04	3.45	0
Tachinus laticollis Grav.	2.60	0	0	11.20	0	0	1.64
Oxypoda skalitzkyi Bernh.	2.08	0.99	0	4.98	0	0.66	3.28
O. umbrata (Gyll.)	0	0.33	0	9.13	0	0.33	0
O. annularis (Mann.)	4.17	3.29	0	0.41	0.94	2.63	0
Liogluta micans (Muls. & Rey)	88.02	6.41	0	0	1.89	0	0
Atheta arctica (Thoms.)	0	0.49	0	13.28	0	0	3.29
A. palustris (Kisenw.)	0	1.15	0	11.20	0	0.82	4.92
A. fallaciosa (Sharp)	0	0	0	8.71	0	0	3.29
A. myrmecobia (Kr.)	0	0.33	0	12.03	0.94	0	1.64
A. fungi (Grav.)	57.29	6.25	3.48	12.03	8.49	0.66	23.02
Lypoglossa lateralis (Mann.)	6.25	4.77	0	12.86	0.94	0.66	14.80
Drusilla canaliculata (F.)	22.92	4.93	0	0.41	22.64	4.11	0
Zyras humeralis (Grav.)	0	0	0	0	33.02	0.16	1.64
Ground-layer non-predators							
Acrotrichis silvatica Rossk.	18.75	0.99	24.31	4.15	3.77	0	0
A. intermedia (Gillm.)	8.85	1.31	81.60	5.26	0	3.77	4.93
***Micropeplus tesserula* Curtis	0	0.33	0	0	0	0	0
Byrrhidae	1.04	5.76	0	7.05	0	9.87	0
Cortinicara gibbosa (Herbst)	0	0	0	73.44	0	0	46.05
Species developing deep in soil							
All Leiodini	0	0.49	0	12.86	0	1.97	16.45
Soil-dwelling Elateridae	0	1.32	5.21	40.25	0	0.99	103.62
Species associated with rodents							
Sciodrepoides watsoni (Spence)	29.16	1.48	31.25	28.21	40.57	2.30	14.80
Catops alpinus Gyll.	91.00	0	19.09	0.83	10.38	0	0
C. tristis (Panz.)	2.60	0.82	1.74	2.90	3.77	0	0
C. nigrita Er.	39.06	2.63	5.21	0.41	21.70	0.16	0
Species specializing in temporary resources							
Nicrophorus vespilloides Herbst	1.04	0.33	3.47	14.97	0	0.16	9.87
Philonthus succicola Thoms.	1.56	1.15	22.57	3.32	0.94	0	0
Deliphrum tectum (Payk.)	4.16	0.66	1.74	11.20	0.94	0.16	1.64
Lordithon thoracicus (F.)	1.04	1.31	1.74	2.07	0	1.15	3.28
L. lunulatus (L.)	0	0.16	22.57	70.12	0	2.83	6.58
Tachinus pallipes (Grav.)	16.67	0	3.48	4.98	0	0	0
T. proximus Grav.	0	0.48	0	14.52	0	0.66	0
Aleochara moerens Gyll.	0.52	24.34	3.48	23.24	6.60	8.55	23.02
Oxypoda alternans (Grav.)	1.04	0	0	8.29	0	0.33	4.92
Atheta subtilis (Scriba)	14.58	0	15.63	4.15	3.77	0.16	0
A. sodalis (Er.)	18.75	2.63	3.48	18.26	16.04	2.30	4.92
A. gagatina (Baudi)	6.77	2.96	0	2.90	26.41	2.30	18.09

	Site 2 PF-B	PF-A	WT-B	WT-A	Site 3 PF-B	PF-A	WT-A
A. aeneipennis (Thomson)	13.54	2.47	1.74	12.03	3.77	4.77	36.18
A. paracrassicornis Brundin	49.48	14.14	12.15	14.52	18.87	4.11	4.92
Boliochara pulchra (Grav.)	23.44	25.88	0	47.30	71.70	70.89	41.19
Predators living under tree-bark							
***Sericoda quadripunctata* (Deg.)	0	3.78	0	0.41	0	3.78	0
Quedius tenellus (Grav.)	2.08	0.32	8.68	4.56	0	0	0
Phloeonomus lapponicus (Zett.)	0	0.33	3.47	9.54	0	0	1.64
***Paranopleta inhabilis* (Kr.)	0	0	0	0.41	0	0	0
Placusa atrata (Mann.)	0	0	0	9.13	0	0	8.22
Epuraea spp.	0.52	7.89	32.99	71.78	0	2.14	16.45
Pityophagus ferrugineus (L.)	0	1.64	5.21	9.13	0	0.16	1.64
Rhizophagidae	4.69	2.63	157.99	7.47	0	0.66	3.29
***Laemophloeus muticus* (F.)	0	0	0	0.41	0	0	1.64
***Pediacus fuscus* Er.	0	9.87	0	2.49	0	10.36	1.64
***Sphaeriestes stockmanni* (Biström)	0	0	0	6.64	0	0	18.09
Species developing in wood attacked by fungi							
Dictyoptera aurora (Herbst)	0.52	0.33	3.48	6.64	0	0	0
Wood-boring Elateridae	0	1.64	5.21	23.24	0	0.66	37.83
Stagetus borealis Israelson	0	0	0	3.32	0	0	41.19
"All anobiids"	0	0	0	7.88	0	0	44.41
Arpidiphorus orbicularis ((Gyll.)	0.52	0.16	0	4.11	0	0.16	0
***Playrhinus resinosus* (Scop.)	0	0	0	0.41	0	0	0
Species attracted to damaged and dead trees							
Anisotoma spp.	0	1.64	62.50	107.88	0	0.49	83.88
Agathidium spp.	0	0.66	41.67	16.77	3.77	0.49	50.98
Sepedophilus littoreus (L.)	0	0.82	0	11.20	0	0.16	3.28
Scaphisoma agaricinum (L.)	0	1.31	1.74	11.20	0	0	9.87
***Henoticus serratus* (Gyll.)	0	0.82	0	26.56	0	0.16	4.93
***Cryptophagus corticinus* Thoms.	0	0	0	4.15	0	0	0
***Caenoscelis ferruginea* (Sahlb.)	0	5.76	1.74	3.32	0	2.63	3.29
Atomaria pulchra Er.	1.56	15.30	1.74	34.44	0.94	1.64	16.44
Cartodere constricta (Gyll.)	0	2.31	0	12.86	0	1.64	6.58
Corticaria rubripes Mann.	1.04	12.83	0	88.80	0	6.91	34.54
C. ferruginea Marsh.	0	15.13	0	318.67	0	3.45	80.60
***Stephanopachys substriatus* (Payk.)	0	0	0	0.41	0	0	0
***Acmaeops marginata* (F.)	0	0	0	0	0	0	1.64
***Hylobius abietis* (L.)	5.21	17.43	0	4.15	24.53	24.18	6.58
Hylurgops palliatus (Gyll.)	0	1.64	3.49	4.15	0	0	4.93
Hylastes brunneus Er.	7.29	20.39	45.14	48.96	2.83	10.86	52.63
H. cunicularius Er.	5.21	15.46	78.12	39.00	0	0	0
H. opacus Er.	0	1.48	0	11.62	0	0.99	37.83
Polygraphus poligraphus (L.)	0	0.49	0	22.82	0	0	0
Pityogenes chalcographus (L.)	0	1.32	8.68	57.26	0	0.33	9.87
Dryocaetes hectographus Reitter	0	11.02	52.08	73.44	0	2.63	1.64
Trypodendron lineatum (Ol.)	0	0.33	3.49	17.43	0	0.16	4.93
All scolytids	14.58	53.45	234.37	385.89	2.83	14.97	139.80
Herbivores							
Galerucella sagittariae (Gyll.)	0	10.70	0	75.93	0	1.31	27.96
Otiorhynchus nodosus (Muller)	0	3.45	0	0.41	0	0.66	0
O. scaber (L.)	1.04	1.32	0	0	1.89	3.29	4.93
Polydrusus ruficornis (Bonsd.)	0	0.82	1.74	0	1.89	6.41	3.29
Strophosoma capitatum (Deg.)	1.56	0.33	0	0	0	6.08	29.60
Predators living on vegetation							
Anthophagus omalinus Zett.	0.52	1.15	13.88	31.95	0	0.48	37.83
A. caraboides (L.)	0	0.48	0	9.96	0	0.48	37.83
Scirtidae	0	1.81	3.47	304.56	0	1.15	210.53
Cantharidae	1.04	0.33	52.08	36.10	0	0.49	42.76
Anaspidae	0	0	43.40	4.15	0	0	0

Table 3, continued	Site 2				Site 3		
	PF-B	PF-A	WT-B	WT-A	PF-B	PF-A	WT-A
Species associated with agriculture							
Perigona nigriceps (Dej.)	0	0	0	0.41	0	0	0
Cryptopleurum subtile Sharp	0	0	0	2.07	0	0	0
Ptiliola brevicollis (Matth.)	0	0	0	0.41	0	0	0
Philonthus rectangulus Sharp	0	0	0	0.41	0	0	0
P. ebeninus (Grav.)	0	0	0	0.41	0	0	0
Gabrius appendiculatus Sharp	0	0.16	0	2.07	0	0	1.64
Atheta laticollis (Steph.)	0	0	0	0.41	0	0	0
Oligota inflata (Mannh.)	0	0	0	0.41	0	0	0
Monotoma picipes Herbst	0	0	0	0.82	0	0	0
M. longicollis (Gyll.)	0	0	0	0.41	0	0	0
Carpophilus marginellus Motsch.	0	0	0	0.41	0	0	0
Cryptophagus pseudodentatus Bruce	0	0	0	0	0	0	3.28
Atomaria lewisi Reitt.	0	0	0	4.56	0	0	1.64
Enicmus histrio Joy & Tomlin	0	0	0	0.41	0	0	0
Typhaea stercorea (L.)	0	0	0	0.41	0	0	0

These fire specialist species do not form a homogenous group. The group includes a predator and a non-predator living in litter, predators living under bark of trees, and species developing in dying or dead wood, as well as ones attracted to wood-rotting fungi (Tables 2–3). Clearly many ecologically quite different types of beetles are attracted to burnt forests.

3.3. Ground-layer predators

Ground-beetles increased at all sites after the fire. One known ground-layer fire specialist, *Amara nigricornis,* was taken at site 1. Possibly some of the carabid species did not actually increase in numbers; instead, their catchability increased as the ground-layer was burnt. However, *Pterostichus adstrictus* appears to be a true fire specialist as its numbers increased at all sites. This may hold for *Bembidion grapii* as well. The only ground-beetle showing any sign of decrease after the burning was *Pterostichus rhaeticus*, which is a species living in habitats with *Sphagnum* mosses, and specimens found were no doubt strugglers from the bogs surrounding sites 2 and 3.

Most dominant litter-inhabiting staphylind beetles suffered heavily because of the fire: *Arpedium quadrum*, *Liogluta micans* and *Zyras humeralis* at site 1 and *Tachinus laticollis*, *L. micans*, *Atheta fungi*, *Drusilla canaliculata* and *Z. humeralis* at sites 2–3. *Zyras humeralis* is an abundant ant-dependent staphylinid beetle in Finnish coniferous forests. Its numbers dropped drastically at all sites after the fire. The same fate befell *Liogluta micans*, another dominant litter staphylinid not associated with ants. Only two staphylinid species belonging to this group, *Mycetoporus lepidus* and *Lypoglossa lateralis,* increased after the fire at all sites. Additional increasing species at sites 2–3 were *Gabrius trossulus*, *Acidota crenata*, *Oxypoda umbrata*, *Atheta arctica*, *A. palustris*, *A. fallaciosa* and *A.myrmecobia*. In most cases this increase was best seen in WT samples, suggesting that the specimens were immigrants.

The two dominant litter-dwelling predatory beetle groups, Carabidae and Staphylinidae, appeared to react quite differently to the burning. Whereas ground-beetles increased nearly invariably, staphylinids showed several different patterns. The superdominant ground-beetle in Northern coniferous forests, *C. micropterus*, seemed to have returned to close to its original numbers after two years — at least more successfully than did other carabids. The fact that almost no ground-beetle species appeared to suffer after the fire may be an indication of trapping bias rather than a reflection of true densities.

3.4. Ground-layer non-predators

All the species belonging to this group reacted strongly to the fire. At all sites the numbers of

Table 4. Sites 2 and 3, Pohjois-Karjala. Combined pitfall and window trap catches before (B) and after (A) the burning, number of specimens per 1000 trapping days per year. Only species found in excess of 60 exx. are included.

	Site 2				Site 3			
	1987–88-B	89-A	90-A	91-A	87–88-B	89-A	90-A	91-A
Ground-layer predators								
Bembidion grapii Gyll.	0	1.88	6.11	9.00	0	2.00	1.15	1.50
Pterostichus adstrictus Esch.	0	0.63	9.17	13.33	0	0.67	6.15	8.85
Calathus micropterus (Duft.)	7.20	16.88	55.00	6.00	38.00	102.67	61.15	11.54
Mycetoporus lepidus (Grav.)	3.60	1.25	23.89	15.67	1.00	3.33	13.46	12.31
Ischnosoma splendidum (Grav.)	5.60	6.25	0.56	3.00	17.00	6.67	0.38	3.85
Liogluta micans (Muls. & Rey)	67.60	0	4.44	7.00	2.00	0	0	0
Atheta fungi (Grav.)	44.80	10.63	11.94	1.67	9.00	9.33	0.77	0.77
Drusilla canaliculata (F.)	17.60	3.75	2.50	6.40	24.00	2.67	1.15	6.92
Ground-layer non-predators								
Acrotrichis silvatica Rossk.	20.00	10.00	0	0	4.00	0	0	0
A. intermedia (Gillm.)	25.60	17.50	3.61	0.33	0	4.00	0	0.38
Cortinicara gibbosa (Herbst)								
Species associated with rodents								
Sciodrepoides watsoni (Spence)	29.60	15.00	2.50	14.67	43.00	6.00	0.77	4.62
Catops alpinus Gyll.	74.00	0.63	0	0.33	11.00	0	0	0
C. nigrita Er.	31.20	2.50	3.33	1.00	0	0	0.38	0
Species specializing in temporary resources								
Nicrophorus vespilloides Herbst	0.80	1.25	15.56	11.67	0	1.33	0	1.92
Lordithon lunulatus (L.)	5.20	9.34	12.50	40.00	0	0	0.38	2.31
Aleochara moerens Gyll.	0.80	115.63	3.33	0	7.00	33.33	4.23	1.92
Atheta sodalis (Er.)	15.20	3.12	11.11	5.00	17.00	9.33	1.92	3.08
A. gagatina (Baudi)	5.20	13.13	0.28	1.00	28.00	4.00	0.77	6.54
A. aeneipennis (Thomson)	10.80	15.63	8.06	0	4.00	4.67	16.92	0
A. paracrassicornis Brundin	40.80	64.38	1.94	3.67	20.00	15.33	1.15	0.78
Boliochara pulchra (Grav.	18.00	136.25	10.28	5.33	76.00	261.33	11.15	13.46
Predators living under tree-bark								
Epuraea binotata Reitt.	0.80	26.25	1.39	0	0	2.00	0	0
Rhizophagus ferrugineus (Payk.)	36.00	2.50	4.17	5.00	0	1.33	0	0.38
Pediacus fuscus Er.	0	36.25	1.67	0.67	0	35.33	1.92	1.15
Species attracted to damaged and dead trees								
Anisotoma axillaris Gyll.	4.00	6.25	3.89	22.33	0	0.67	1.54	2.69
A. glabra (Kugel.)	6.40	5.63	24.17	13.67	0	1.33	9.61	2.31
Agathidium confusum Bris.	2.40	10.00	3.89	12.67	0	0	0	0
Henoticus serratus (Gyll.)	0	36.88	2.50	0.33	0	2.67	0	0
Caenoscelis ferruginea (Sahlb.)	0.40	4.37	5.00	6.00	0	0	3.46	3.46
Atomaria pulchra Er.	0.80	80.62	11.39	1.67	1.00	10.67	0.78	0.78
Corticaria rubripes Mann.	0.80	123.12	23.61	3.33	0	12.67	10.38	6.54
C. ferruginea Marsh.	0	427.50	48.61	0.33	0	38.00	5.00	0
Hylobius abietis (L.)	4.00	39.37	13.61	1.00	26.00	52.67	23.46	4.23
Hylastes brunneus Er.	16.00	1.25	30.00	10.67	3.00	1.34	20.77	16.15
H. cunicularius Er.	22.00	7.50	33.61	18.30	0	0	0	0
H. opacus Er.	0	0	7.22	3.67	0	0	9.61	1.54
Pityogenes chalcographus (L.)	2.00	23.12	54.72	4.00	0	4.67	0.38	0
Dryocaetes hectographus Reitter	12.00	10.63	34.17	34.67	0	0.40	0	6.15
Herbivores								
Galerucella sagittariae (Gyll.)	0	107.50	13.33	9.33	0	6.67	3.91	2.31
Strophosoma capitatum (Deg.)	1.20	0	0	0.67	1.00	6.00	5.00	12.69
Predators living on vegetation								
Anthophagus omalinus Zett.	6.00	39.37	4.44	1.67	0	8.67	1.15	4.23
Cyphon kongsbergensis Munst.	0.40	15.62	9.44	1.67	0	14.00	1.15	2.69
C. variabilis (Thunb.)	0	1.25	22.50	6.00	0	1.33	11.54	5.38
C. punctipennis Sharp	0.40	131.25	52.22	65.00	0	2.66	3.08	3.85
C. padi (L.)	0	6.25	13.05	3.00	0	4.00	19.61	7.30
Absidia schoenherri (Dej.)	8.40	6.25	2.50	4.00	0	4.00	1.54	1.54

moss-feeding Byrrhidae increased dramatically. This may be an artefact, however, as the destroyed ground-layer must have forced these beetles to move around. However, as they clearly increased in window trap samples as well, they probably were truly attracted to burnt areas. Similarly, *Cortinicara gibbosa* became numerous at sites 2–3. This group included two losers as well: the tiny *Acrotrichis* species abundant in litter suffered drastic losses because of the fire. They had not regained their numbers two years after the fire, possibly because of changes in the litter structure.

3.5. Species developing deep in soil

After the fire, at all sites the soil-dwelling elaterids increased dramatically. Most of them were caught with window traps, suggesting they were immigrants. They were probably attracted to the area because forest-fires release nutrients that encourage the growth of grasses and weeds, on roots of which the elaterid-larvae feed. A similar increase could be seen in the numbers of Leiodini species, which develop in subterranean mycorrhizae. Possibly the fire stimulated fungal growth, thus increasing potential Leiodini breeding-sites.

3.6. Species associated with rodents

Most cholevids were abundant at the sites before the fire and practically non-existent afterwards. As this could be observed at all sites, it clearly is a phenomenon typical of forest-floor burning. Most of these species develop in the burrows of rodents. Apparently the disappearance of the beetles is a reflection of the impact of the fire on the rodent population. The only species still caught in considerable numbers after the fire was *Sciodrepoides watsoni* at sites 2–3 in window traps. As it had greatly diminished at the same sites in pitfall catches, these specimens were most likely immigrants. The cholevids showed some increase two years after the fire, but their pattern was ambiguous.

3.7. Species specializing in temporary resources: mushrooms, dung and carrion

This fairly large group included both losers and winners. At site 1 all the three species increased after the fire. They form a fairly homogenous group — all of them feeding primarily on diptera larvae developing in mushrooms. Ecologically similar species at sites 2–3: *Lordithon* spp., *Tachinus* spp., *Aleochara moerens*, *Oxypoda alternans* and *Bolitochara pulchra*, all benefitted from the fire as well — some very much so. Other species commonly encountered in mushrooms, i.e. *Deliphrum tectum*, *Atheta sodalis* and *A. aeneipennis,* increased in window trap catches, but diminished in pitfall catches. This pattern was seen in the carrion specialist, *Nicrophorus vespilloides*, as well. The species preferring dung, such as *Philonthus succicola*, *Atheta subtilis* and *A. paracrassicornis,* all suffered from the fire.

Most of the species, especially those living in mushrooms, peaked immediately after the fire.

3.8. Predators living under bark of trees

This group includes the largest number of fire specialist caught: *Sericoda quadripunctata*, *Paranopleta inhabilis*, *Laemophloeus muticus*, *Pediacus fuscus*, *Rabocerus foveolatus* and *Sphaeriestes stockmanni*. These species live as predators under the bark of trees damaged or killed by fires. It appears quite likely that they feed on the scolytids, cryptophagids and latridiids attracted to the same trees, although the role of the cucujids is unclear.

All the known scolytid predators caught, *Phloeonomus lapponicus*, *Quedius tenellus*, *Placusa atrata* and *Epuraea* spp., increased substantially in numbers after the fire as well. The only species diminishing was *Rhizophagus ferrugineus* — this trend was observed at site 2 only and may thus be an artefact. At site 3 there was a slight increase, whereas at site 1 the material was inconclusive. Both the decline of *Rhizophagus* and the increase of *Epuraea* took place immediately after the fire.

3.9. Species developing in wood attacked by fungi

The larvae of these beetles develop in dead wood infested by fungi. Their numbers increased after the fire at sites 2 and 3, especially in window-trap catches. This can be seen at site 1 as well with respect to wood-boring elaterids. The increase in these beetles appears to be due to the fire, as it undoubtedly created new potential breeding-sites. The increase in the numbers of beetles belonging to this group is to be expected only 2 to 4 years after a fire and was only indicated at site 1.

3.10. Species associated with damaged and dead trees

This is a heterogeneous and undoubtedly unnatural assemblage of species. All of them are attracted to damaged trees, however. Many true fire-specialists placed in this group were caught: *Henoticus serratus*, *Cryptophagus corticinus*, *Caenoscelis ferruginea*, *Stephanopachys substriatus*, *Acmaeops marginata*, *Hylobius abietis* and *H. pinastri*. Practically all species included in the group benefitted from the fire.

The small species belonging to the families Cryptophagidae and Latridiidae are associated with the various microhabitats within damaged tree-trunks, all of them probably living on fungi. It is possible that these beetles actually bring fungal spores with them when invading a tree — especially as they appear immediately after the fire. They all increased after the fire at all sites. However, the changes were not identical, suggesting different fungi as resources for different species.

At all sites, the numbers of scolytids and curculionids breeding under the bark increased. *Agathidium* and *Anisotoma* species associated with wood-fungi started to increase only 2 years after the fire.

The observed increases in numbers of these groups were clearly connected with the fire, as the availability of potentially useful microhabitats after the burning increased.

3.11. Herbivores

Several chrysomelids and curculionids breeding on immigrant plants and on small saplings of deciduous trees increased in numbers after the fire. This is of course a reflection of the natural succession after a forest fire. The most dramatic change was the immediate massive influx of *Galerucella sagittariae* at site 2 (Table 4), most of the specimens being caught with window traps (Table 3). This species feeds on the plant *Rubus chamemorum.*

3.12. Predators living on vegetation

Most predators living freely on vegetation decreased after the fire. The *Anthophagus* species diminished in site 1, but increased in sites 2–3. The strong increase in the number of scirtids at sites 2 and 3 may be an artefact, as no such phenomenon occured in site 1; the larvae of scirtids develop in water in the bogs surrounding th study sites. Possibly a favourable warm summer coinciding with the burning experiment produced the very high numbers of *Cyphon* in the Pohjois-Karjala sites. On the other hand, this increase may have been due to the changed trapping conditions. Possibly the scirtids are able to fly much more freely in the burnt forest. This effect, if present, should have been more pronounced at sites 2 and 3, these being only about a hectare in size, whereas site 1 was some five hectares in size with considerably less edge effect.

3.13. Species associated with agriculture

Perhaps the most surprising result was the finding of numerous compost species at sites 2 and 3 after the fire. The list is so long that it can not be explained as chance: *Perigona nigriceps*, *Cryptopleurum subtile*, *Ptiliola brevicollis*, *Philonthus rectangulus*, *Philonthus ebeninus*, *Gabrius appendiculatus*, *Atheta laticollis*, *Oligota inflata*, *Monotoma picipes*, *Monotoma longicollis*, *Carpophilus marginellus*, *Cryptophagus pseudodentatus*, *Atomaria lewisi*, *Enicmus histrio*, *Typhaea stercorea*. No such species were found at site 1. Differences in large-scale distribution do not explain this, as most of the species in question are found in the general area around site 1 (Muona & Viramo 1986). The fact that compost-loving species are attracted to recently burnt areas appears sensible, however, the blackened soil contributes to an especially warm microclimate. We suggest that the presence of the compost species is a real feature of the burnt forest in agriculturally active areas. Although definite values are not available to us, the areas around sites 2 and 3 appear to have much more ongoing agricultural activity than does the area surrounding site 1.

Many of the compost species caught were originally immigrants to Europe from Japan or Eastern Pacific Siberia. If these so-called adventive species are really attracted to burnt areas, this may have contributed to their ability to cross the Siberian taiga on their way to Europe from east Asia. Thus these animals may be ecologically very similar to fire-specialists. If corroborated in future studies, this would suggest that both the opportunistic adventive species and the highly specialized fire-loving beetles of the primeval forests may in fact be in a sense identical — both groups exploiting short-lived, disturbed, patchy environments.

4. Conclusions

Our preliminary studies support the traditional view that Scandinavian forests contain a high number of species attracted to burnt areas (e. g. Lundberg 1984). Although trapping methods, especially pitfalling, are poorly suited for studying changes drastically altering the structure of vegetation, it nevertheless appears clear after burning at all sites that both the number of specimens and species increased. Many groups benefitted from the impact of the fire, e.g. predators living in litter and mushrooms, wood-boring and soil-dwelling species as well as the true fire-specialists. The marked increase in both predators and in non-predators utilizing polypores as well as mushrooms suggests that increased fungal growth is an important factor in succession after forest fires.

Several species strongly diminished in Finland were attracted to the burnt sites, especially in Pohjois-Karjala. Clearly the fires simulated true forest fires fairly well. This being the case, such burning could and should be done more extensively in Finland. Numerous fire-specialists are included in the Finnish Red list. Apparently many of them still occur in small numbers in the forests. In order to secure their future, a comprehensive burning plan is required.

Acknowledgements. Mr. J. Palosaari and Mrs. T. Patosalmi helped JM in the gathering and sorting of the material. The Finnish Forest and Parks Service was responsible for the execution of the actual burning and provided financial support for the experiment at site 1. The comments of Mr. J. Siitonen and Mr. I. Mannerkoski greatly improved the manuscript.

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Appendix. Systematic list of genera with species listed in the tables.

Carabidae: *Notiophilus, Miscodera, Patrobus, Bembidion, Pterostichus, Calathus, Sericoda, Agonum, Amara, Perigona*
Dytiscidae: *Agabus*
Hydrophilidae: *Cryptopleurum*
Ptiliidae: *Ptiliola, Acrotrichis*
Leiodidae: *Leiodini, Anisotoma, Agathidium*
Cholevidae: *Nicrophorus, Sciodrepoides, Catops*
Staphylinidae: *Gabrius, Philonthus, Quedius, Xantholinus, Phloeonomus, Deliphrum, Acidota, Coryphium, Anthophagus, Scaphisoma, Mycetoporus, Ischnosoma, Lordithon, Sepedophilus, Tachinus, Aleochara., Oxypoda, Liogluta, Athea, Lypoglossa, Drusilla, Zyras, Boliochara, Placusa, Oligota*
Lycidae: *Dictyoptera*
Elateridae: Wood-boring species: *Lacon, Harminius, Denticollis, Ampedus, Melanotus*
Soil-dwelling species: *Selatosomus, Anostirus, Eanus, Orithales, Limonius, Sericus, Athous, Dalopius*
Anobiidae: *Stagetus*
Nitidulidae: *Epuraea, Carpophilus, Pityophagus*
Sphindidae: *Arpidiphorus*
Monotomidae: *Monotoma*
Cucujidae: *Pediacus*
Cryptophagidae: *Henoticus, Caenoscelis, Cryptophagus, Atomaria*
Latridiidae: *Cartodere, Enicmus, Corticaria, Cortinicara*
Mycetophagidae: *Typhaea*
Salpingidae: *Rhabocerus, Sphaeriestes*
Anaspidae: *Anaspis*
Cerambycidae: *Pogonocherus*
Chrysomelidae: *Galerucella*
Curculionidae: *Otiorhynchus, Polydrusus, Strophosoma, Hylobius, Pissodes*
Scolytidae: *Hylurgops, Hylastes, Polygraphus, Pityogenes, Dryocaetes, Trypodendron*