

Clear-cutting before burning prevents establishment of the fire-adapted *Agonum quadripunctatum* (Coleoptera: Carabidae)

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Received 5 January 1995, accepted 1 April 1995

Breeding populations of the fire-adapted carabid-beetle *A. quadripunctatum* were found in most of the fifteen investigated burned, uncut forests, but not in any of the fifteen burned clear-cuts, although a few immigrants were found in two of them. The proportion of open-habitat carabid species progressively increased during the two first seasons after both clear-cutting and prescribed burning. These species are spring breeders in contrast to the summer-autumn breeding species found in the forest. Populations of carabids, and other beetles as well, were more or less unaffected by an experimental low intensity fire. The possibility that surviving open-habitat carabid species on burned clear-cuts prevent *A. quadripunctatum* from establishing successful breeding populations is discussed.

1. Introduction

Several insect species breed exclusively in newly burned forests. Typically, fire-adapted insects reproduce in burned areas for only one or a few years after fires (Evans 1971, Lundberg 1984, Wikars 1992, Muona & Rutanen 1994). The reason for this is largely unknown but it has been suggested that these species are competitively excluded later on during succession (Danks and Footitt 1989).

Forest fires used to be the dominant successional force in post-glacial boreal forests. Large-scale forest fires of high intensity occurred at inter-

vals of 50 to 200 years (Heinselman 1973, Zackrisson 1977, Engelman 1984). Less intense fires covering smaller areas occurred with shorter intervals (Johnson 1992). Nowadays however, forest fires have become rare as a result of active fire suppression and removal of dead trees, which can serve as ignition sites during thunderstorms (Romme and Despain 1989). During this century, clear-cutting and soil scarification have replaced fire and stormfelling as the major disturbance over large regions of boreal forest. This is especially true in NW Europe, where forestry is intense, and almost all productive forests are managed (e.g. Esseen et al. 1992). There is an ongoing debate about how to

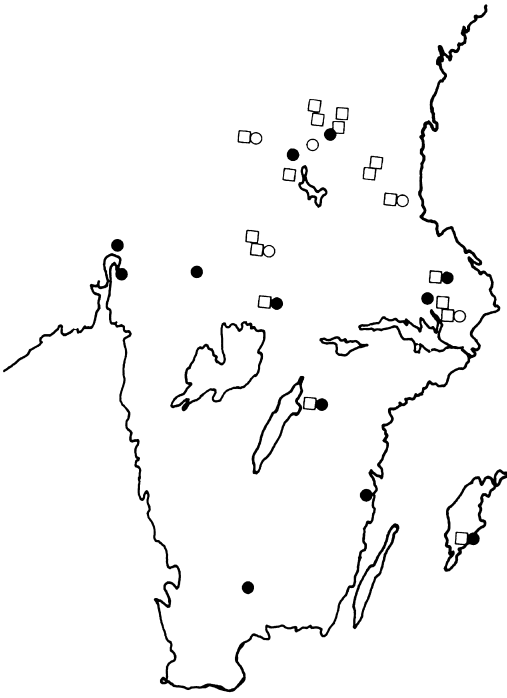


Fig. 1. Occurrences (filled symbols) of *Agonum quadripunctatum* in burned uncut forest (circles) and on burned clear-cuts (squares) in Middle-south Scandinavia.

maintain biodiversity in the managed forest (Hansen et al. 1991). One way to help maintain biodiversity would be to use forestry practices that mimic natural disturbance regimes. In areas frequently disturbed by fires, clear-cutting followed by slash-burning could be utilized. In contrast, in fire-refuge areas selective cutting should be given preference (Hansen et al. 1991, Zackrisson & Östlund 1991, Angelstam et al. 1993, Hunter 1993).

Many fire-adapted insects have vanished or become endangered in NW Europe during the 20th century (Heliövaara and Väisänen 1984, Ehnström et al. 1993). Consequently, prescribed burning has been proposed as a method to favour fire-dependent species (Granström 1991, Angelstam et al. 1993). Prescribed burning of clear-cuts is a well known regenerative method, at least in Fennoscandia (Wretling 1932, Lundmark 1988) However, the actual significance of burning clear-cuts for conservation purposes has not been assessed.

This paper reports on the occurrence of the fire-adapted carabid-beetle *Agonum (Sericoda) quadripunctatum* De Geer, (Coleoptera: Carabidae) on burned clear-cuts and in burned, uncut forest. The success of *A. quadripunctatum* in burned areas could depend on the composition of the total carabid assemblage and to what extent other carabid species survive fires. The carabid assemblages in burned and unburned sites are compared and the effect of different fire intensities on carabids is studied in a field experiment.

2. Materials and methods

2.1. Survey of *Agonum quadripunctatum*

A. quadripunctatum is a small (body length 6–7 mm), mainly ground-living predator with a circumpolar distribution. It can become very abundant one to two seasons after forest fires, but disappears one or two seasons later (Winter 1980, Burakowski 1986, Ehnström 1991, Holliday 1991, Wikars pers. obs.). The beetle is day-active over a wide range of temperatures. It is a spring breeder (Lindroth 1986), and when reproduction is over in June a period of low adult activity follows that lasts until August. The new generation emerges in late August–September and the species is again active before hibernation (Winter 1980, Lindroth 1986).

The occurrence of *Agonum quadripunctatum* (presence or absence) was surveyed in 26 recently burned areas in Scandinavia (57–62°N, 11–18°E, Fig. 1). Areas included both uncut and clear-cut forests subjected to wild-fires or prescribed burning. Most areas burned in June–July or May, and one in September. Eight burned areas included both uncut and clear-cut forest. The forest areas ranged in size from 0.5 to 160 ha and clear-cuts from 5 to 100 ha. Information about recent cutting operations (if any) were obtained from local foresters. The clear-cuts had been cut one or two winters before they were burned. Three areas were partly clear-cut shortly after the fires. Habitat parameters such as tree-canopy cover, ground moisture, and vegetation were recorded during visits.

The inventories were made one or two growing seasons after the fires. Most areas were visited at least two times. The occurrence data refer to observations of active beetles. Additionally, in most areas the upper ground substratum (3–5 cm) was sieved if the weather permitted. Sieved samples were either examined directly in the field or extracted in Tullgren-funnels in the laboratory. It was assumed that the species had been able to reproduce successfully if it could be found with this sampling effort. In all cases either none or more than ten individuals were found.

To assess the immigration of *A. quadripunctatum* ten to twenty flight-barrier traps were put up one or a few days

after the fires in four of the areas and operated until autumn. The traps consisted of aluminium buckets (9 × 12 cm, 5 cm deep) filled with a 50% mixture of ethylene glycol and water. A detergent and a denaturing substance (Bitrex®, to avoid predation from vertebrates), were added. Above each bucket a transparent piece of PVC-plastic (10 × 15 cm) was placed vertically as a flight-intercept. The traps were attached to lying as well as standing tree-trunks.

2.2. Successions of carabid assemblages

Successions of carabid assemblages were studied during two seasons by pitfall trapping after clear-cutting, as well as after selective cutting followed by prescribed burning. The study was made at Rödmyrberget (61°06'N, 16°03'E, 380 alt.), in Central Sweden. An adjacent uncut forest stand served as the control. Mortality caused by the fire was estimated by comparing numbers and species composition with the control before and after burning.

Clear-cut, not burned site: Effects of forest cutting were studied on a 15 ha area clear-cut in January 1990. Before cutting, the forest was dense and dominated by Norway spruce (*Picea abies*), with some trees older than 140 years. Aspen (*Populus tremula*), birch (*Betula pubescens*) and pine (*Pinus silvestris*) were present in equal numbers and together made up 40% of the timber. The underlying soil consisted of a very coarse moraine with some patches of peat. There was hardly any herb layer the first year, and the ground was covered with mosses (*Hylocomium splendens*, *Dicranum* spp.) which gradually died off. During the second year, herbs and grasses began to sprout. In July 1991 the soil was scarified by harrowing in all but the most stony parts, where digging was used.

Selectively cut, burned site: A 6 ha area was selectively (50% of the standing timber) cut in January 1989. In 30 May 1990 the site was subjected to prescribed burning. The dominating tree species was spruce, of which the largest trees were removed. Birch and pine constituted 30% of the timber in the forest and were left uncut. The vegetation before burning was similar to that of the uncut forest (see below). The fire intensity was high due to a large amount of cutting debris. The fire killed all vegetation except for some large pine trees. Much of the moraine layer was combusted, resulting in a substantial destruction of rhizomes and seeds. One year after the fire, more than 50% of the ground was still bare of vegetation.

Uncut site: The control site was a 25 ha old-growth stand (max. ca 250 yr) in direct contact with the burned site and with a similar composition of tree species. The ground substrata of both the uncut and burned site was a coarse moraine containing a large proportion of sand. Along the borders toward plantations, small shrubs like *Calluna vulgaris*, *Vaccinium vitis-idea*, and *V. myrtillus* dominated. Mosses, e. g. *Hylocomium splendens* and *Dicranum* spp., dominated in the forest interior.

In each area, carabids were sampled continuously using two rows of five pitfall traps (aluminium buckets,

12 × 20 cm wide, 5 cm deep, filled with a liquid (see above)). The distance between traps was 10 m in a row and 50 m between rows. Masonite roofs pinned on large nails were used to avoid rain-flooding of the traps. Flight-barrier traps attached to trees (see above), were used to sample arboreal species. They were of the same number and placed in similar positions as the pitfall traps.

Samples from the selectively cut site (pre-fire sample) and uncut forest were taken in May 1990. Then all three sites were sampled from late May to late September 1990 and from late April to late September 1991. All traps were emptied on the same day, at 2 to 6 week intervals. The sampling season was divided into four periods that differed slightly in timing and duration between the two years. May (1990: 3/5–30/5 and 1991: 29/4–3/6), June (1990: 31/5–11/7 and 1991: 3/6–15/7), July–August (1990: 11/7–23/8 and 1991: 15/7–18/8) and September (1990: 23/8–29/9 and 1991: 18/8–29/9). The burned area was sampled with a shorter interval (2 weeks) immediately after burning.

The nomenclature, habitat preferences and reproductive periods of the carabids found were obtained from Lindroth (1985, 1986). Habitat preference was registered for tree-canopy cover and three categories were recognized; C) closed forest preference, E) eurotype, i.e. no preference, and O) open habitat preference. Additional information about main reproductive periods was obtained from Larsson 1939. All species were classified as either; S) spring breeding, or A) summer-autumn breeding (Appendix 1). Species compositions were compared by summarizing the number of individuals (irrespective of species) in each category.

2.3. Experimental fire effects on survival

Survival of carabid beetles was investigated following a prescribed burning on 4 June 1991 of a 2 ha intact forest in Haraldstjärn, Älvdalen (61°06'N, 16°03'E, alt. 540 m), in Central Sweden. The forest was dominated by pine, growing on well-drained moraine. The vegetation of the field- and bottom layer was mosaic and dominated by *Vaccinium vitis-idaea*, *Calluna vulgaris*, *Cladonia* spp. and *Pleurozium screberii*. The burning was not very intense due to a quite moist humic layer and the absence of cutting debris and large woody debris. Shortly after the fire three 4 m² plots were enclosed. This was done by digging down masonite fences 10 to 15 cm deep in the soil which were covered with nets of 1 mm mesh-size. The carabids in each enclosure were sampled until late August by four pitfall traps in each.

Additional fifteen 0.25 m² enclosures of a similar construction were used to test the impact of different fire-intensities. Five were unburned due to excessive watering (20 mm/unit area) before burning. Five were unmanipulated, and another five had their fire-intensity increased by the addition of 2.00 kg/m² of dry twigs before the burning. A pit-fall trap and an emergence trap in each enclosure oper-

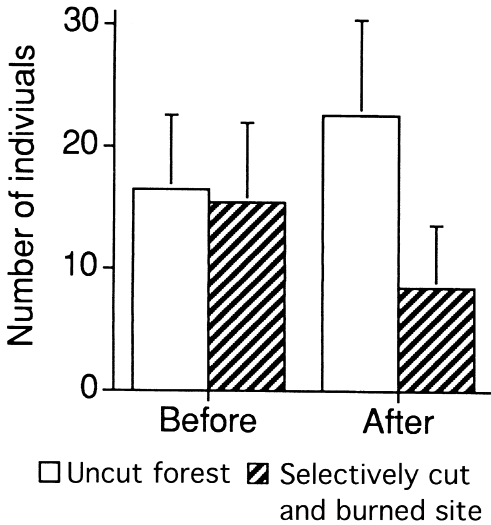


Fig. 2. The number of carabids caught in pit-fall traps ($N = 10$) 4–5 weeks before and after burning the selectively cut site and in an uncut control-site at Rödmyrberget. Error bars indicate one *S.D.*

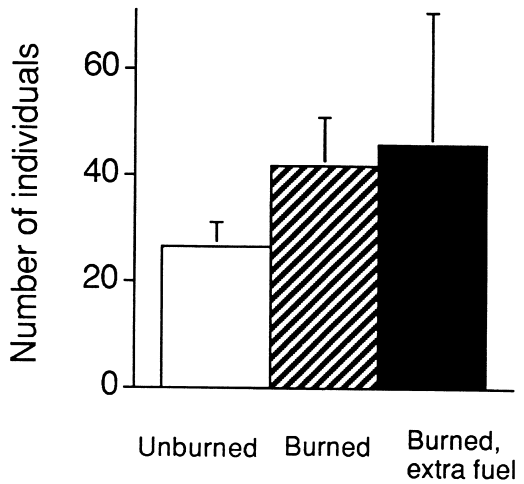


Fig. 3. The number of ground-living beetles caught in enclosures burned with different intensity at Haraldstjärn. Error bars indicate one standard deviation. $N = 5$ in each category.

ated from 5 June to 29 August. The emergence trap, that mainly collects positively phototactic insects, was placed at the top of the tent-like net; and was made of an inverted plastic jar with an inlet made by a plastic funnel.

3. Results

3.1. The occurrence of *Agonum quadripunctatum*

A clear preference for burned forest over burned clear-cuts was found (Fig. 1, presence/absence; clearcut = 0/17, forest = 12/5, *G*-test, $G > 17$, $P < 0.0001$). Four out of the five uncut forests where the species were absent were exceptionally small (0.5–1 ha) and surrounded by clear-cuts. The species was present in all areas that were clear-cut after burning ($N = 3$). In three areas (two clear-cuts, one forest) single individuals were caught shortly after the fire, but none later on.

3.2. Fire-mortality effects

During five weeks after the prescribed burning at Rödmyrberget the number of carabids in the traps

was lower than in the control (Fig. 2, $t = -4.81$, $df = 18$, $P < 0.0001$). Before burning no difference was found ($t = 0.39$, $df = 18$, $P = 0.70$). If the majority of the beetles caught shortly after fire were immigrants, this ought to have been reflected as an increase during sampling. However, the number of carabids did not differ between 31/5–16/6 and 16/6–7/7 (paired *t*-test, $t = -0.82$, $df = 18$, $P = 0.42$).

In the three large (4 m²) enclosures 9, 9 and 21 carabids were found after the experimental burning at Haraldstjärn which gives a mean density of 3.25 inds/m². The numbers in the small enclosures were too few to evaluate the survival rate. Instead all ground-living beetles were counted and analyzed (excluding phytophagous species living above ground). Ground-living beetles (mainly Staphylinidae, Cryptophagidae and Latridiidae) can be presumed to suffer the same mortality as carabids. No differences were found in the number of beetles in the enclosures on differently burned plots. In fact there was a tendency that the five unburned plots had fewer beetles than the ten burned plots (Wilcoxon two-sample test, $Z = -1.90$, $df = 1$, $P = 0.06$, Fig. 3). The number of beetles in the two groups of plots burned with different intensity did

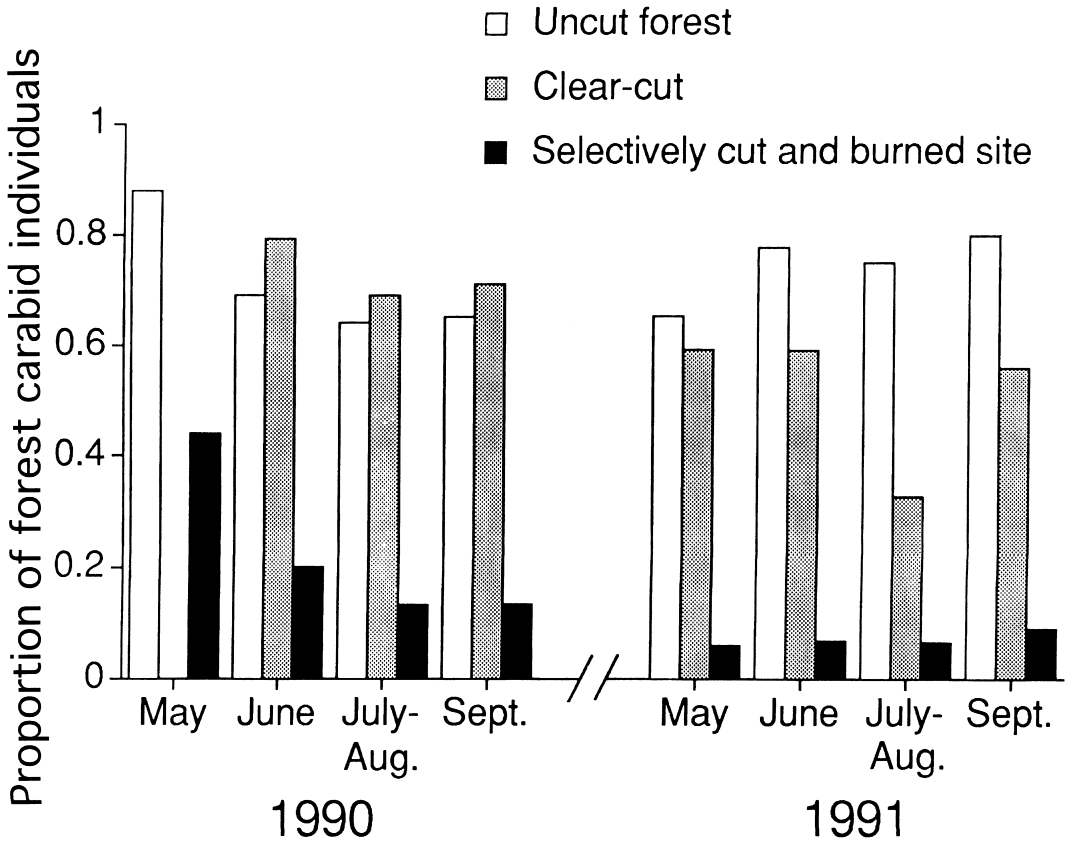


Fig. 4. Proportion of forest-carabid individuals caught during two seasons in the selectively cut-burned area, clear-cut and uncut forest at Rödmyrberget. First sampling after burning occurred in June 1990.

not differ (Wilcoxon two-sample test, $Z = -0$, $df = 1$, $P = 1.00$).

3.3. Species composition of carabids

The comparisons of species composition had two goals. First, to analyze the habitat preferences of carabids in disturbed and undisturbed habitats, and second, to study if, and when, forest-living carabids are replaced by other species after disturbance.

Before burning more open-preferring carabid individuals were found in the selectively cut site compared with the uncut forest at Rödmyrberget ($G = 51$, $df = 1$, $P < 0.0001$). At the fresh clear-cut the community was composed of carabids with a similar habitat preference as those of the forest (1990, $G = 0.05$, $df = 1$, $P = 0.82$), but one year later the clear-cut had more open-preferring

carabid individuals than the forest (1991, $G = 146$, $df = 1$, $P < 0.0001$).

The amount of carabids in the selectively cut — burned area preferring open habitat did not peak immediately after the fire. Instead a steady decline in the proportion of forest-carabid individuals was found. This was also true for the clear-cut (Fig. 4).

Of the open-habitat species found at Rödmyrberget ($N = 18$), 72% are spring breeders, whereas among the forest-living species ($N = 8$), 75% are summer-autumn breeders ($G = 5.2$, $df = 1$, $P < 0.05$). Nine species were classified as having no habitat preference with regard to tree-canopy cover (Appendix 1). The majority of carabids caught in the disturbed areas were mainly spring breeders, whereas carabids caught in the uncut forest and at the fresh clear-cut were summer-autumn breeders (Fig. 5).

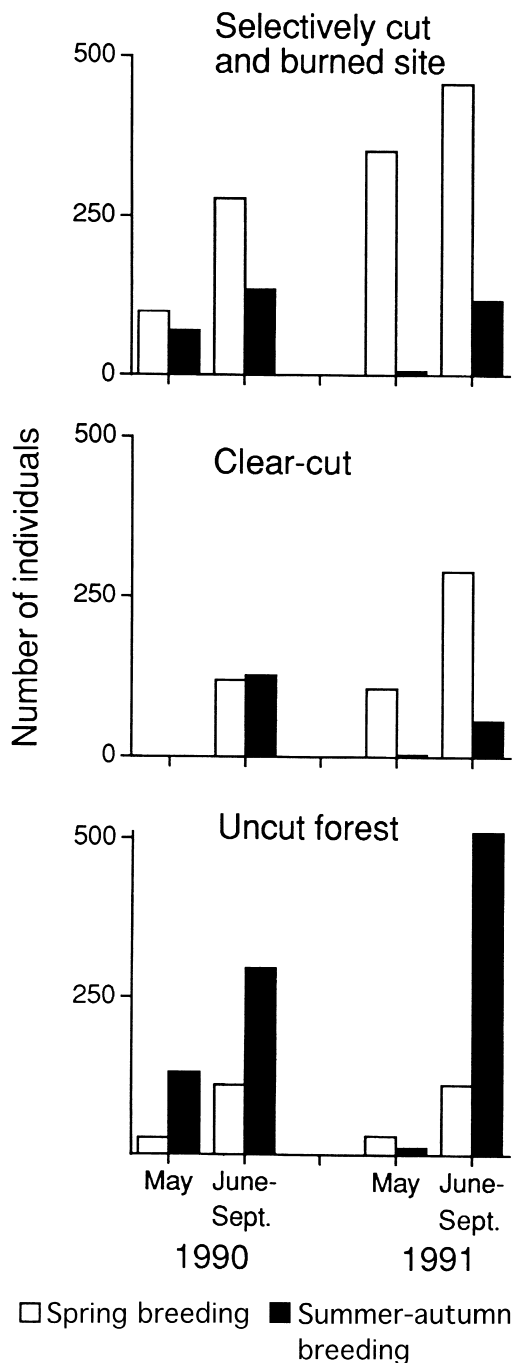


Fig. 5. The catches of spring and summer-autumn breeding carabids caught during two seasons at Rödmyrberget. M = May, J-S = June–September.

4. Discussion

4.1. The occurrence of *Agonum quadripunctatum*

The clear preference for burned, uncut forests over burned clear-cuts was surprising because the species develops in the ground (Burakowski 1986, Baranowski pers. comm.). It can thus hardly be dependent on trees, even if the adults sometimes can be found hibernating or hunting under bark (Lindroth 1986). The chemical composition, moisture of the ground and vegetation could differ between burned forest and burned clear-cuts. However, the great variation in moisture, sun-exposure and depth of mor-layer of burned habitats inhabited by *A. quadripunctatum* suggests that these factors are not crucial to the species.

Furthermore, the species could be food-limited on burned clear-cuts. However, studies from the boreal and temperate zone show increased densities of microarthropods, e. g. springtails, (an important prey item category of *A. quadripunctatum*), in both burned forest and burned clear-cuts (Huhta 1971, Tamm 1986, Winter et al. 1980). Feeding and gut-studies have not found evidence of a specialized feeding mode in *A. quadripunctatum* (Winter et al. 1980, Burakowski 1986). A large amount of needles usually drops to the ground a few days after fires, especially in dense spruce-stands. These needles are often still green when falling, thereby adding a lot of nutrients to the ground, and are able to support dense populations of springtails (Ehnström pers. comm.). However, in my studies I have sometimes found dense populations of *A. quadripunctatum* irrespectively of accumulations of needles on ground.

The presence of the *A. quadripunctatum* on clear-cuts that were cut after burning implies that some biological characteristics other than food availability and abiotic factors are probably important.

4.2. Carabid survival

Very few experimental studies deal with the immediate impact of fire on arthropod mortality (references in Ahlgren 1974, Lyon et al. 1978).

Even if my data lack proper controls, they clearly indicate that a substantial part of the ground-living fauna, including carabids, survives fires. Generally, the mortality of ground-living arthropods seems directly related to the combustion of the litter and organic soil during the fire (e.g. Bellido 1987). This seems especially true in boreal habitats, where organic soil-layers are thick and wet (Van Cleve et al. 1986).

The anomalous result from Haraldstjärn (Fig. 3), where the lowest density of ground-living beetles was obtained in the unburned patches, presumably reflects the importance of the micro-climate. At this site, being at an altitude of 540 m, insect activity is certainly limited by temperature. The cooling effect of adding excessive water probably resulted in the low number of beetles caught. The humid and 5–7 cm thick mor-layer apparently insulated from the heat, even when extra fuel was added. No burning of the mor-layer took place here, probably because of the humid conditions and that the flame-front passed the area rapidly in the wind direction.

The reduced number of carabids at Rödmyrberget (Fig. 2) was obviously caused by the high fire-intensity. The mor-layer was completely combusted over a substantial part of the area, but even here a large fraction of the carabid fauna seemed to have survived. The burning was made against the wind with a slow progress of the flame-front. Some large carabids (e. g. *Carabus violaceus*) could be seen running away from the flames, probably escaping into safe patches.

Earlier studies have indicated that some carabids survive even high intensity wild-fires (Winter 1980, Spires and Bendel 1983, Holliday 1984). Muona and Rutanen (1994) found that all carabid species survived prescribed burnings of low intensities, and some forest species in fact increased in numbers in trap catches afterwards.

4.3. Effects of disturbance on carabid-community composition

The composition of carabid communities did not immediately diverge to a maximum degree after a disturbance. As abiotical conditions are changed immediately by disturbances one could expect

the fauna to respond fast. Instead there seemed to be a more gradual replacement of forest species by species adapted to open conditions. This was especially true for clear-cuts, where the forest-carabid community partially seemed to be intact the first season after cutting (see also Lenski 1982, Niemelä et al. 1993, Haila et al. 1994).

A successive replacement of species also seemed valid after burning. Thus, the species composition at Rödmyrberget continued to alter during the second season, as also reported from a wildfire-area in Canada (Holliday 1991). In Holliday's 11 year study, the difference in species composition was most pronounced in the third, and not the second season, after the fire (no sampling was done the same year as the fire). Subsequently the community returned into the pre-fire situation. This suggests that carabids survived the fire and that the forest fauna was gradually replaced. Huhta (1971) found that burning caused a much faster change from original conditions in spider communities than clear-cutting only. Surviving spider populations were present during the first season after burning, but disappeared the following season. Maximum differences in species similarity, and the greatest proportion of open-habitat species, were found seven years after both prescribed burning and clear-cutting.

Generally, post-fire environmental changes, rather than the immediate mortality effects of fires, are the primary cause to the change in ground-living fauna composition (Ahlgren 1974, Lyon et al. 1978).

Clear-cutting is followed by a successive immigration and establishment of open-habitat species. Because burning of clear-cuts rarely kills all carabids, an open-adapted fauna is present immediately after the fire. Furthermore, if it is important to fire-adapted species to become breeding pioneers, this could be the reason for their absence on burned clear-cuts. On the other hand, when these insects colonize a burned forest they encounter a fauna that suffers from the changed conditions. The dry ground conditions may make forest carabids unable to breed, for example due to an early larval mortality because of desiccation (Goulet 1974).

There seems to be a general relationship between the timing of reproduction and habitat pref-

erence among carabids. Thus, spring breeders are dominant in exposed habitats (Larsson 1939). As *A. quadripunctatum* is a spring-breeder, the potential for competition would be greater in burned clear-cuts where open-preferring species reproducing at the same time of the year dominate, compared to newly burned forest, where summer-autumn breeding species dominate. In his review on competition among carabids, Niemelä (1993) points out the difficulties in detecting interspecific competition in nature. It is hard to imagine that food is in short supply soon after forest fires, especially in boreal areas, where the impact of burning on primary production usually is positive (Ahlgren 1974, Danks & Footitt 1989). Priority-effects, i. e. when the establishment order of species has a significant impact on the composition of the future species assemblage (Drake 1990), may be especially important to early successional species as *A. quadripunctatum*. In predatory animals the mechanism could be intraguild predation (Polis & Holt 1992). It can simply be that older larvae (being larger) eat their smaller guild companions, as has been reported for dragon-flies (Johansson 1993). However, if competition or intraguild predation determines the absence of *A. quadripunctatum* from burned clear-cuts can only be evaluated after field experiments.

Acknowledgments. I thank Y. Haila, M. Loraue, J. Niemelä, P. Punttila, B. W. Svensson and S. Ås for constructive criticism on previous drafts of the paper. S. Lundberg helped with species identifications. World Wildlife Fund gave financial support. The forestry companies Domän, Orsa Forest Common and Stora Skog performed prescribed burnings.

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Appendices

Appendix 1. Number of carabid beetles caught in different habitats and periods. *Months*: M = May, J–S = June to September. *Reproduction*: S = main reproduction during spring, A = reproduction during summer and autumn. *Habitat preference*: C = closed forest, E = no preference and, O = open habitat. Observe that the "selectively cut-burned site" was unburned in May 1990. Numbers in parantheses under "Total" refer to beetles caught in flight-barrier traps.

AREA YEAR MONTHS	Selectively cut-burned site		Clear-cut site				Uncut forest				TOTAL			
			1990		1991		1990		1991					
			M	J–S	M	J–S	J–S	M	J–S	M		J–S		
SPECIES	Repro		Habitat		duction		pref.							
<i>Acupalpus parvulus</i> (Sturm)	S	O	0	0	0	2	0	0	0	0	0	0	0	2 (2)
<i>Agonum quadripunctatum</i> (DeG.)	S	E	0	2	0	0	0	0	0	0	0	0	0	2 (2)
<i>Amara brunnea</i> (Gyll.)	A	C	7	6	0	1	6	0	2	3	1	0	1	27 (0)
<i>A. lunicollis</i> Schiödt	S	O	0	0	1	2	1	0	2	0	0	0	1	7 (0)
<i>A. nigricornis</i> Thoms.	S	O	0	0	1	12	1	0	16	0	0	0	0	30 (4)
<i>Bembidion bruxellense</i> Wesm.	S	O	0	1	0	0	0	1	0	0	0	0	0	2 (1)
<i>B. lampros</i> (Hbst.)	S	O	1	2	0	1	0	0	0	0	0	0	0	4 (0)
<i>B. grapii</i> Gyll.	S	O	1	1	2	4	2	0	0	0	0	0	0	10 (5)
<i>Bradycellus caucasicus</i> (Chaud.)	S	O	0	1	0	1	2	0	2	2	0	0	0	8 (6)
<i>Calathus micropterus</i> (Dft.)	A	C	33	37	2	16	85	2	24	18	214	11	432	974 (12)
<i>Carabus glabratus</i> Payk.	A	C	3	4	1	3	0	0	0	4	4	0	0	19 (0)
<i>C. hortensis</i> L.	A	C	0	3	0	3	11	0	8	0	14	0	9	48 (2)
<i>C. violaceus</i> L.	A	E	5	9	0	27	6	1	10	1	29	0	18	106 (6)
<i>Cychrus caraboides</i> (L.)	A	C	1	0	0	0	10	1	7	3	0	0	2	24 (1)
<i>Cymindis vaporariorum</i> (L.)	A	O	0	0	0	0	0	0	0	2	0	0	0	2 (2)
<i>Dromius agilis</i> (F.)	S	E	1	1	0	0	5	0	1	1	17	0	10	36 (22)
<i>D. fenestratus</i> (F.)	A	E	0	0	1	1	0	0	0	0	6	0	0	8 (8)
<i>D. sigma</i> (Rossi)	S	O	0	0	0	0	0	0	1	0	0	0	0	1 (1)
<i>Harpalus quadripunctatus</i> Dej.	S	O	3	7	1	15	4	1	6	0	0	0	0	37 (6)
<i>H. solitarius</i> Dej.	S	O	0	1	0	2	0	0	0	0	0	0	0	3 (0)
<i>Leistus ferrugineus</i> (L.)	A	O	1	9	0	2	1	0	0	0	14	1	4	32 (0)
<i>L. terminatus</i> (Hellw.)	A	C	0	4	0	3	0	0	0	0	0	0	0	7 (0)
<i>Miscodera arctica</i> (Payk.)	A	O	0	4	0	3	0	0	3	0	0	0	0	10 (0)
<i>Notiophilus aquaticus</i> (L.)	A	O	0	3	1	0	0	0	0	0	0	0	0	4 (0)
<i>N. biguttatus</i> (F.)	S	E	18	13	7	18	13	8	28	8	45	9	48	215 (3)
<i>N. germinyi</i> Fauv.	A	O	4	13	0	20	0	0	1	0	4	0	3	45 (1)
<i>N. reitteri</i> Sphaeth	S	C	2	1	0	1	2	0	0	0	12	8	20	46 (2)
<i>Patrobis assimilis</i> Chaud	A	E	0	0	0	0	3	0	0	0	0	0	0	3 (0)
<i>P. atrorufus</i> (Ström)	A	E	12	14	0	7	2	0	1	0	7	0	35	78 (0)
<i>Pterostichus adstrictus</i> Eschztz.	S	O	40	241	320	380	16	33	83	5	22	3	17	1160 (39)
<i>P. niger</i> (Schall.)	A	E	3	28	1	31	2	0	0	0	3	0	5	73 (0)
<i>P. oblongopunctatus</i> (F.)	S	C	28	6	19	15	70	62	148	11	15	9	15	398 (4)
<i>P. strenuus</i> (Pz.)	S	E	4	1	1	0	0	0	0	0	0	2	1	9 (0)
<i>Tachyta nana</i> (Gyll.)	S	O	1	0	0	2	2	0	2	0	0	0	0	7 (7)
<i>Trechus rubens</i> (F.)	S	O	0	0	0	2	1	1	1	0	0	0	0	5 (2)
TOTAL			168	412	358	574	245	110	346	58	407	43	621	3442 (138)
Number of species			19	25	13	26	21	9	19	11	15	7	16	35 (22)