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Ground beetle (Coleoptera: Carabidae) responses to a forest wildfire in northern Europe

Реакции жужелиц (Coleoptera: Carabidae) на лесной пожар в Северной Европе

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КЛЮЧЕВЫЕ СЛОВА: лесной пожар, пирофильные жужелицы, Carabidae

ABSTRACT. Carabid beetles were studied for two years following an extensive wildfire in a pine forest area with shallow soil close to Stockholm. The beetles were collected in pitfall traps placed at six plots along a 1.2-km line-transect from the unburnt forest (control) to the centre of the burnt area. Two of the plots in the centre of the area differed in fire behaviour. The pyrophilous carabids *Sericoda quadripunctata* and *Pterostichus quadrifoveolatus* became readily dominating, of which *S. quadripunctata* seemed to be favoured by severe burning and *P. quadrifoveolatus* by weak burning. Close-to-water-habitat specialists were fairly common during the first spring after the fire, probably because they could survive the fire in swampy depressions. The carabids were more abundant and rich in species in the least severely burnt area than in the unburnt forest or in the severely burnt plots. Even the carabids classified as forest species were more commonly collected in the weakly burnt area than in the forest, which might be explained by higher carabid mobility due to less ground vegetation than in the forest. The number of species did not differ in a consistent way between the unburnt and burnt forest. The weakly burnt forest might have served as a partial refuge during the fire and might also have kept a greater amount of prey than the more severely burnt areas. Fire severity rather than distance to the forest edge seemed to determine the population densities during the first two years after the fire.

РЕЗЮМЕ. В течение двух лет изучали сообщества жужелиц после сильного пожара в сосновом лесу на слаборазвитых почвах в окрестностях Стокгольма (Швеция). Жуков собирали с помощью ловушек Барбера, расположенных на шести участках по трансекте длиной 1,2 км от негорелого леса (контроль) к центру пожарища. Два участка в центре пожарища различались по силе выгорания. Пирофильные жужелицы *Sericoda quadripunctata* и *Pterostichus quadrifoveolatus* вскоре после пожара стали доминантами, причем *S. quadripunctata* встречалась в основном на сильно, а *P. quadrifoveolatus* — на слабо выгоревших участках. Околоводные виды были обычны в течение первой весны после пожара, вероятно из-за того, что они пережили пожар в болотистых понижениях в лесу. Наибольшая численность и разнообразие жужелиц были отмечены на слабо выгоревших участках по сравнению с сильно выгоревшими и нетронутым лесом. Даже лесные виды были более многочисленны на слабо выгоревших участках по сравнениюс с лесом, что может быть объяснено более высокой мобильностью жужелиц на пожарище из-за отсутствия мохово-лишайникового покрова. Количество видов не отличалось между пожарищем и негорелым лесом. Слабо сгоревший лес мог выступать в качестве убежища во время пожара и содержать значительно большее количество пищевых ресурсов по сравнению с сильно выгоревшими участками. Интенсивность пожара, а не расстояние до края леса определяли плотность популяций жужелиц на пожарище в течение двух лет после пожара.

Introduction

Natural forest fires have been an extensive and recurrent phenomenon in boreal forests of Northern Europe [Zackrisson, 1977; Niklasson & Granström, 2000]. A diverse set of organisms needs fires, especially insects and fungi [Esseen et al., 1997]. Due to efficient fire suppression, the area affected by wildfire has decreased more than 100-fold during the last 100 years in Sweden. Many fire-dependent species have experienced range contractions, and a few of them have already gone nationally extinct [Gärdenfors, 2000; Kotze & O'Hara, 2003]. Prescribed fires by forestry and conservation agencies are today regularly made in Sweden for conservation purposes to favour fire-dependent species [Granström, 2001].

Wildfires are extremely variable, and the effects will depend on both deterministic and stochastic factors [Johnson & Miyanishi, 2001; Certini, 2005]. For soil-dwelling arthropods, the burning of the organic soil by glowing fires in the humus layer will determine to what extent the organisms survive [Ahlgren, 1974; Wikars & Schimmel, 2001]. The amount of soil consumption will, in turn, depend on soil moisture before the fire [Schimmel & Granström, 1996]. However, soil burning also differs between dry and wet vegetation types [Ryan, 2002]. The post-fire assemblage will presumably depend on to what extent the fauna has survived, the immigration capacity of the fauna and vegetation succession. Spatial patterns during colonisation may be important if a large area is affected by fire, but have seldom been reported.

Several studies have been made on carabid beetles following forest fires in boreal forest. Most studies have compared unburnt and burnt forests or focussed on the post-fire succession [Winter, 1980; Richardson & Holliday, 1982; Gardner & Usher, 1989; Holliday, 1992; Muona & Rutanen, 1994; Wikars, 1995; Fernández Fernández & Salgado Costas, 2004; Saint-Germain et al., 2005]. However, few studies have focussed on the effects of the heterogeneity within a recently burnt area on carabid beetles.

The aim of this study was to determine the effects of a wildfire on carabid beetles in central Sweden. We hypothesized that fire-dependent species should be quick invaders in the area, be favoured by fire severity and prefer the central part of the fire, whereas other species should recover more slowly and gradually increase their populations from the edge of the surrounding, unaffected forest towards the fire centre.

Materials and methods

Study area

In August 1999, a wildfire affected an area of 450 ha in the central part of Tyresta National Park and Nature Reserve, which together make up 4700 ha of predominantly coniferous forests. The area is situated 20 km south of Stockholm in central Sweden (59°10′ N, 18°20′ E). Mean annual temperature and precipitation is 6.6 °C and 539 mm, respectively, at the nearest meteorological station in Stockholm. The area is heterogeneous because of numerous fissure valleys. Protruding areas consist of undulating rocky outcrops, and mires/swamps and lakes fill the depressions. A sparse forest of Scots pine (*Pinus sylvestris* L.) and common silver birch (*Betula pendula* Roth) is growing on the outcrops, whereas the mire elements are to a large extent covered by Scots pine and hairy birch (*Betula pubescens* Ehrh.). The pine forest is dominated by 150–300 year-old trees and has never been affected by large-scale forestry. Norway spruce (*Picea abies* (L.) Karst.) and aspen (*Populus tremula* L.) mostly grow on slopes and seldom form stands in the burnt area.

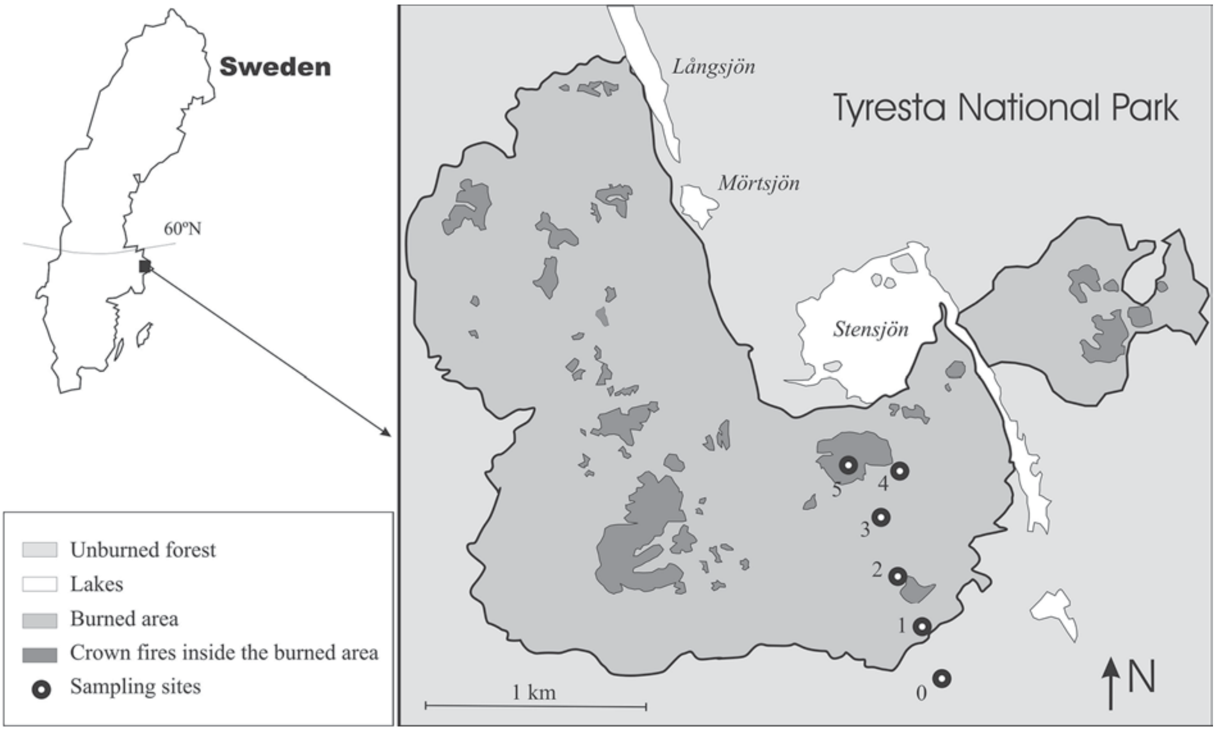

Fig. 1. The study area in Tyresta National Park (Sweden) affected by a wildfire in 1999. Arabic numbers — tha sampling plots.
Рис. 1. Район проведения исследований — национальный парк Тюреста (Швеция), на территории которого в 1999 г. произошёл лесной пожар. Арабскими цифрами обозначены учётные площадки.

A long drought preceded the fire in 1999, and warm and windy weather made the fire intense, and it burnt deeply into the soil. The shallow organic soils on the bedrock were to a large extent burnt away, whereas the peat soils in the moist depressions were reduced, but seldom completely burnt. Crown fires affected 5% of the burnt area (Fig. 1), estimated from aerial photographs taken shortly after the fire [Granström, pers. comm.]. Despite this, the fire killed more than 90% of the trees because of serious root injuries and subsequent blow-downs. In December 1999, a storm felled more than 80% of the trees, and winter storms in 1999–2001 felled even more [Wikars, own observation].

Sampling plots

Carabid beetles were sampled at six different plots, 30x30 m, one unburnt (0) and five burnt plots (1–5) during 2000–2001 (Table 1, Fig. 1). The control plot (0) consisted of a pine forest ca. 200 m from the edge of the burnt area. A line transect that represented a gradual increase in distance (plots 1–3) from the forest edge was established, and at the end of this transect two plots with contrasting fire behaviour (plots 4 and 5) were chosen.

Plot 4 had less burning depth than the other burnt plots. This plot, representing an area of 1 ha, was dominated by Norway spruce and had the highest crown density of the plots investigated. Plot 5 was placed in a ca. 6 ha intensively burnt area. Crown fires had affected this rather elevated area, which contained only a few small wet depressions, but the burning depth was not exceptional compared with the other burnt plots.

All plots had some variation in moisture conditions. In the drier parts, *Cladina/Cladonia* lichens, *Calluna vulgaris* (L.) Hull. and *Vaccinium vitis-idaea* L. had probably grown before the fire, as judged from the regrowth observed after the fire by the latter two species [Schimmel & Granström, 1996] and by comparison with the vegetation in unburnt areas. In the moister parts, there were *Sphagnum* mosses, *Ledum palustre* L. and *Eriophorum vaginatum* L. (based on vegetative regrowth after the fire). A documentation of the tree layer (including soot-height on trees which indicates fire severity) and vegetation was done in October and November 2001. On these occasions, mosses dominated the vegetation. Dominant herbs were *Chamaenerion angustifolium* Scop.*, Rubus idaeus* L. and *Senecio* spp., together with regenerating species such as *Calluna vulgaris* L., *Vaccinium vitis-idaea* L., and *V. myrtillus* L.

Sampling

Carabid beetles were sampled by 40 Barber pitfall traps consisting of 6 cm wide and 8 cm deep plastic jars that were placed at the level of soil surface. The distance between traps was 3–5 m. The jars were filled with 50% propylene glycol and a detergent. Ten traps were placed within the control plot and six traps were placed at each of the other plots. The traps were emptied every 4–8 weeks. In 2000 we sampled from April 14 to November 14, and in 2001 from May 26 to November 7. During 2000, which was a wet year, some of the traps were filled with rainwater. A few traps were destroyed by animal activity. Consequently, the estimates had to be based on fewer than 40 traps on some occasions.

Species identification was undertaken using appropriate keys [Kryzhanovskij, 1965; Lindroth, 1985, 1986]. The nomenclature follows Kryzhanovskij et al. [1995].

Table 1. Description of sampling plots after the wildfire in Tyresta.
Таблица 1. Описание пробных площадок после лесного пожара в национальном парке Тюреста.

	Unburnt	Burnt				
	0	1	2	3	4	5
Distance from edge (m)	200	50	250	450	~500	~500
Relative crown cover (%) [1,2]	55	75	70	60	100	60
Pine/birch/spruce (%)[2]	70/20/10	95/5/0	85/10/5	90/10/0	15/15/70	88/4/8
Proportion of windthrows (%) [3]	0	80	50	75	50	75
Peat-soil on moist subplot [2]	yes	no	yes	yes	no	no
Organic layer remaining (%) [4]	-	<10	10-20	10-20	>20	<10
Fire intensity [5]	-	2.25±0.34	3.22±0.48	3.75±0.57	2.61±0.33	8.30±0.45

1 Crown cover < 20 m from the sampling plot.
2 For burnt plots pre-fire conditions were estimated.
3 The proportion of trees (based on crown cover) lying on ground on 10 October 2001.
4 Measured < 5 m from the sampling plot.
5 Maximum soot height (m) on pine stems < 20 m from the sampling plot (mean ± SE, n = 10).
1 Сомкнутость крон < 20 м на пробных площадках.
2 Для горевших площадок оценены условия, предшествующие пожару.
3 Доля деревьев (оценивалась по сомкнутости крон), лежащих на земле 10 октября 2001 г.
4 Оценено < 5 м на пробную площадку.
5 Максимальная высота сажи (м) на стволах сосен < 20 м на пробную площадку (среднее ± SE, n = 10).

Each species was ascribed to one of the following four ecological groups: close to water habitat specialists, pyrophilous, forest, or open-habitat species [Lindroth, 1992]. The observations were grouped into three seasonal periods. In 2000 these periods were April 14 – June 2 (spring), June 2 – August 26 (summer) and August 26 – November 14 (autumn), and in 2001 they were May 26 – July 1 (spring), July 1 – August 23 (summer) and August 23 – November 7 (autumn). Species occurrence was mainly expressed as the number of individuals caught per trap and day (catchability). Species exceeding 10% of the abundance of an assemblage were considered dominant.

Statistical treatment

To examine the effects of burning on carabid beetles, we performed a two-way ANOVA with location and time as factors. Based on the outcome of the ANOVA, we could judge whether there was (1) a difference between non-burnt and burnt plots, (2) an effect of distance to the unburnt forest edge, (3) a difference between slightly (>20% of the organic layer remaining) and severely (<10% of the organic layer remaining) burnt plots (plots 4 and 5, respectively) and (4) a difference between seasons and years. Since the transect used was not replicated, the conclusions are formally restricted to this particular transect. On the other hand, since there was no indication of a clear distance effect, plots 1, 2, 3 and 5 can be seen as replicates within the moderately/severely burnt area, whereas plot 4 represents an unreplicated example of an area with strong crown fire but weak soil combustion. A one-way ANOVA was performed separately for two pyrophilous species to unravel the influence of the burning depth on their catchability. Shannon, Simpson and Berger-Parker indices were used to explore quantitative and qualitative changes of carabid beetle assemblages [Magurran, 1992]. Pearson similarity was used to compare the species composition of different plots. For the two fire-specialized species, a canonical correspondence analysis was undertaken to illustrate the correlations to different factors performed by using Statistica 6.0.

Results

Temporal changes

In all 1285 individuals of carabid beetles from 22 genera and 40 species were caught, of which 17 were classified as forest, 11 were close to water habitat specialists, 10 open habitat, and 2 pyrophilous species (Table 2).

The abundance of carabids decreased from 2000 to 2001 (F=4.615, p=0.039), the first and second years following the fire (Fig. 2). The pyrophilous species *Sericoda quadripunctata* and *Pterostichus quadrifoveolatus* dominated the carabid assemblages at the burnt plots (Fig. 3). These species were frequently collected during springtime in both 2000 and 2001, but there was an insignificant decline with time from the summer and autumn of 2000 to that of 2001 (Fig. 3). Close to water habitat specialists and forest species also declined, and were captured in lower proportions in 2001 than in 2000 (Table 2).

Distance to forest edge

In the unburnt area the catchability was very low in both years (Figs 2–3), and a total of 14 species were found (Table 2). The carabid assemblage mostly consisted of typical forest species (86%) with a high share of close to water habitat specialists. Based on the diversity indices, the carabid assemblage of the control plot was the most even.

The cluster analysis separated the carabid communities from the unburnt (plot 0) and burnt areas (plots 1–5). The burnt edge (plot 1) of both sampling years had ca. 73% similarity to other burnt plots, while the similarity varied from 93 to 97% within this group (Fig. 4).

Carabids were, in general, caught in insignificantly higher numbers at the five burnt plots than in the control plot during both years (Fig. 2). The burnt plots (especially plot 1) had varying species composition. At plot 1, open-habitat species, such as *Bembidion lampros* Herbst, were as abundant as pyrophilous species, whereas the latter group clearly dominated at all other burnt plots (Table 2).

There was no significant difference of plot position along the transect and its catachability (F=2.053, p=0.117), except for some carabid species. The pyrophilous *S. quadripunctata* gradually increased in abundance towards the centre of the burnt area (F=19.504, p<0.001). The other pyrophilous species, *P. quadrifoveolatus,* showed no clear trend along the transect (Fig. 5).

The canonical correspondence analysis showed that the only factor correlating with *S. quadripunctata* along both ordination axes was fire severity (Fig. 6). *P. quadrifoveolatus* was only connected with crown area and remaining soil. There was a positive correlation between this species and soil depth (F=7.875, p=0.021). Other factors and correlations for *S. quadripunctata* were non-significant. Nevertheless, *P. quadrifoveolatus* was also positively correlated with fire severity along axis 1, indicating a connection to fire severity.

Fire severity

Different fire behaviour and effect on soil organic layer (Table 1) seemed to affect the number of trapped carabids. At the slightly burnt plot 4, the carabid catchability was higher than in any other plots (Figs 2–3) (F=8.920, p=0.006). Forest species were found at higher numbers in plot 4 than in any other plots including the control forest (Fig. 3, Table 2). The pyrophilous *P. quadrifoveolatus* was also found in high numbers at this plot (Fig. 5B). The adjacent crown-fire plot 5 had similar abundances of carabids as other well-burnt plots (1–3), but here *P. quadrifoveolatus* had low numbers whereas *S. quadripunctata* had as high numbers as at plot 4 (Fig. 5A). The latter species constituted 59–74% of all carabids at this plot compared with 12–51% at the other burnt plots, making the carabid assemblage at plot 5 highly unbalanced in relation to the other plots (Table 2).

Table 2. Number of carabid beetles captured in pitfall traps at the unburnt (0) and burnt (1–5) plots in Tyresta National Park during 2000 and 2001.
Таблица 2. Количество жужелиц, отловленных почвенными ловушками в 2000 и 2001 гг. на негоревшем (0) и горевших (1–5) площадках в национальном парке Тюреста.

Species	2000						2001						
	0	1	2	3	4	5	0	1	2	3	4	5	
Pyrophilous species, no. of individuals	0	54	73	135	286	72	1	22	31	39	93	68	874
Pterostichus quadrifoveolatus Letzner, 1852	–	31	32	65	191	10	1	16	12	24	58	12	457
Sericoda quadripunctata (De Geer, 1774)	–	23	41	70	95	62	–	6	19	15	35	56	412
Forest species, no. of individuals	18	5	8	11	110	25	20	5	3	2	47	8	268
Nebria brevicollis (Fabricius, 1792)	–	–	3	1	1	9	–	2	–	2	–	1	19
Notiophilus biguttatus (Fabricius, 1779)	2	4	1	4	14	1	3	1	1	–	17	–	49
N. germinyi Fauvel, 1863	–	–	–	–	–	–	4	–	–	–	–	–	4
Carabus hortensis Chaudoir, 1863	–	–	–	–	3	–	–	–	–	–	1	–	5
C. violaceus Linnaeus, 1758	–	–	2	–	–	1	–	–	1	–	4	3	11
Cychrus caraboides Linnaeus, 1758	–	–	–	–	1	–	1	–	–	–	–	–	2
Loricera pilicornis (Fabricius, 1775)	–	–	1	–	–	–	–	–	1	–	–	–	2
Miscodera arctica (Paykull, 1790)	–	–	–	–	–	–	1	–	–	–	–	–	1
Epaphius secalis (Paykull, 1790)	5	–	–	–	1	–	2	–	–	–	1	–	9
Patrobus assimilis Chaudoir, 1846	6	–	1	–	–	–	2	–	–	–	–	–	9
Pterostichus niger (Schaller, 1783)	3	–	–	–	13	11	1	–	–	–	3	4	35
P. oblongopunctatus (Fabricius, 1787)	–	–	–	–	54	1	–	–	–	–	18	–	73
Calathus micropterus (Duftschmid, 1812)	2	–	–	5	20	2	6	2	–	–	2	–	39
Amara brunnea (Gyllenhal, 1810)	–	–	–	–	3	–	–	–	–	–	–	–	5
Dicheirotrichus placidus (Gyllenhal, 1827)	–	1	–	–	–	–	–	–	–	–	–	–	1
Harpalus quadripunctatus Dejean, 1829	–	–	–	–	–	–	–	–	–	–	2	–	3
Dromius schneideri Crotch, 1871	–	–	–	1	–	–	–	–	–	–	–	–	1
Close to water habitat species, no.of individuals	3	4	28	12	0	3	4	1	0	3	0	0	58
Notiophilus aquaticus (Linnaeus, 1758)	–	–	–	–	–	–	1	–	–	–	–	–	1
N. palustris (Duftschmid, 1812)	–	–	–	–	–	–	1	–	–	–	–	–	1
Dyschiriodes globosus (Herbst, 1783)	1	1	–	–	–	2	1	–	–	–	–	–	6
Bembidion obliquum Sturm, 1825	–	–	3	–	–	–	–	–	–	–	–	–	3
B. quadrimaculatum (Linnaeus, 1761)	–	–	1	–	–	–	–	–	–	–	–	–	1
B. rupestre Wesmael, 1835	–	–	2	2	–	–	1	–	–	–	–	–	5
Pterostichus diligens (Sturm, 1824)	2	–	16	1	–	1	–	–	–	–	–	–	20
P. nigrita (Paykull, 1790)	–	–	6	4	–	–	–	–	–	3	–	–	13
Agonum viduum (Panzer, 1797)	–	3	–	4	–	–	–	–	–	–	–	–	7
A. thoreyi Dejean, 1828	–	–	–	1	–	–	–	–	–	–	–	–	1
Acupalpus flavicollis (Sturm, 1825)	–	–	–	–	–	–	–	1	–	–	–	–	1
Open–habitat species, no. of individuals	0	38	6	5	0	5	0	21	2	7	5	0	89
Cicindela campestris Linnaeus, 1758	–	1	1	–	–	–	–	–	–	–	–	–	2
Bembidion lampros (Herbst, 1784)	–	36	1	2	–	1	–	19	2	3	–	–	64
Agonum sexpunctatum (Linnaeus, 1758)	–	–	3	2	–	–	–	–	–	2	–	–	7
Olisthopus rotundatus (Paykull, 1790)	–	–	–	–	–	1	–	–	–	–	–	–	1
Amara cursitans Zimmerman, 1832	–	–	–	–	–	2	–	–	–	–	5	–	7
A. lunicollis Schiödte, 1837	–	1	1	–	–	–	–	–	–	–	–	–	2
Anisodactylus binotatus (Fabricius, 1787)	–	–	–	1	–	–	–	–	–	–	–	–	1
Acupalpus parvulus (Sturm, 1825)	–	–	–	–	–	–	–	–	–	1	–	–	1
Harpalus rubripes (Duftschmid, 1812)	–	–	–	–	–	1	–	1	–	1	–	0	3
Microlestes minutulus (Goeze, 1777)	–	–	–	–	–	–	–	1	–	–	–	–	1
Total no. of individuals	21	100	115	163	398	105	25	49	37	51	145	76	1285
No. of species	7	9	15	13	11	14	12	9	6	8	11	5	40
Berger–Parker Index (d)	0,29	0,36	0,36	0,43	0,48	0,59	0,24	0,39	0,53	0,47	0,40	0,74	–
Shannon index (H’)	1,79	1,48	1,87	1,43	1,48	1,54	2,32	1,56	1,16	1,46	1,69	0,86	–
Simpson index (C)	0,19	0,28	0,23	0,35	0,31	0,37	0,12	0,28	0,40	0,32	0,25	0,57	–

0 — control; 1 — edge; 2 — 250 m far from the forest; 3 — 450 m far from the forest; 4 — slightly burnt and 5 — severely burnt plots in the centre.
0 — контроль; 1 — край гари; 2 — 250 м вглубь гари; 3 — 450 м вглубь гари; 4 — слабо горевший и 5 — сильно горевшие участки в центре гари.

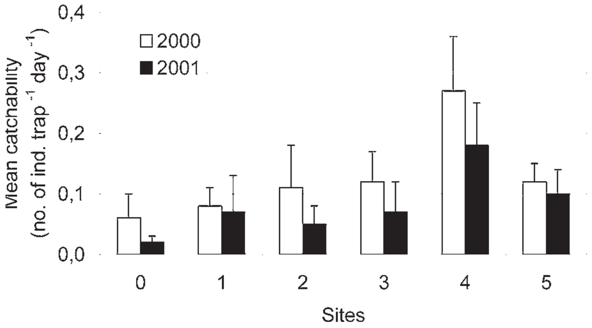

Fig. 2. Catchability of ground beetles in 2000 and 2001 (mean ± SE, n = 6–10).

Рис. 2. Уловистость жужелиц в 2000 и 2001 гг. (среднее ± SE, n = 6–10).

Discussion

Temporal changes

While the characteristics of carabid assemblages in unburnt boreal forests are rather well known [Thiele, 1977; Niemelä et al., 1989; Butterfield, 1997], disturbances like a forest fire will change most of the plot characteristics. The fire in Tyresta National Park was very severe with regard to burning depth. Thus, we assume that the fire killed a great portion of carabids. *S. quadripunctata* appeared in the burnt area immediately after the fire [Wikars, pers. obs.]. This good flier is strongly attracted by chemical substances exuded from burnt wood [Burakowski, 1986; Lindroth, 1992]. Its high abundance in the crown-fire area could be the result of an extra strong attraction to this plot.

Further observations confirmed fire attraction of *S. quadripunctata* and, partly, of *P. quadrifoveolatus*, which turned out to be super-abundant in the burnt area the spring following the fire. Burnt forests attract many other insects [Kolbe, 1981; Wikars, 1992; Schutz et al., 1999] that can serve as food sources for the pyrophilous carabid species. Probably, the lack of competition and potential predators provide these species food, which contributes to their drastic increase in abundance. Other species may gradually start to immigrate into the burnt area and compete with the pyrophilous carabids for preys. The decline in density of the latter group, observed at the end of the study period, may reflect increasing competition. A decline following the two-year period after fire has earlier been observed for *S. quadripunctata* by Holliday [1984] & Ehnström [1991]. However, in our study the number of non-pyrophilous carabids also seemed to decline with time in the burnt area, indicating that these species were not responsible for the decline of the pyrophilous ones (Fig. 3).

A problem with the use of pitfall traps is that their efficiency depends on the structural complexity of the ground surface [Andersen, 1995]. Higher catches in burnt forests are not necessarily an evidence of higher densities, because the reduction of vegetation will increase carabid mobility and, thus, increase the possibility to reach and be captured by a pitfall trap. Therefore, the low number of beetles captured in the unburnt forest (plot 0) possibly did not reflect the real abundance. Slightly lower catches at the burnt plots in 2001 than in 2000 (Fig. 3) can also be an effect of vegetation re-growth, which was substantial in 2001.

Distance to forest edge

The catchability (number of individuals trap^{-1} day^{-1}) was almost as low at the edge plot (plot 1) as at the other burnt plots (Fig. 3). Plot 1 had a deviating species composition with several species associated with open habitats (Table 2). After the fire, some species probably colonised the study area from nearby agricultural areas and clear-cuts. However, the open-habitat species decreased in abundance from the forest edge to the centre of the burnt area. The reason why they did not invade the entire burnt area is not evident, but they probably stopped when they found suitable habitats in the unburnt-burnt ecotone.

Neither forest nor close to water habitat specialists seemed to invade the burnt area. The impact of the nearby forest on the carabid assemblage at the edge plot (1) was weaker than expected from studies on mature forest – open habitat ecotones [Heliölä et al., 2001]. Only single individuals of the close to water habitat specialist *Acupalpus flavicollis* Sturm and the forest species *Dicheirotrichus placidus* Gyll. were found at plot 1. In contrast, the pyrophilous species, which are known to be good dispersers [Burakowski, 1986], had their highest abundance in the centre of the burnt area. Also several other pyrophilous insect species such as the beetles *Melanophila acuminata* Deg. and *Helophorus tuberculatus* Gyll. were common in the centre of the burnt area [Wikars, pers. obs.]. This could be an effect of the increased attraction to crown-fire areas that were mainly located in the centre of the burnt area. However, it could also be a behavioural adaptation to avoid competition, which could be stronger in the edge habitats.

Fire severity

Fire behaviour seemed to be the most important factor influencing the formation of post-fire carabid beetle assemblages. Different plots had experienced variable fire severity with one plot (4) being affected by crown fire but with moderate reduction of the soil organic layer. Furthermore, the burning depth differed substantially between plots, but there were also differences between wet and dry patches within the same plot. At wet patches, the organic soil was not completely burnt, which promoted higher survival at plots 2 and 3, which were surrounded by small bogs. At these two plots, close to water habitat specialists constituted a substantial portion of the carabids during the spring immediately after the fire.

At the slightly burnt plot 4, forest species could have survived to a larger extent than at the other burnt plots. This plot consisted of a dense spruce forest in which the soil before the fire had not dried out as much as in the pine forest. Another factor affecting the greater abun-

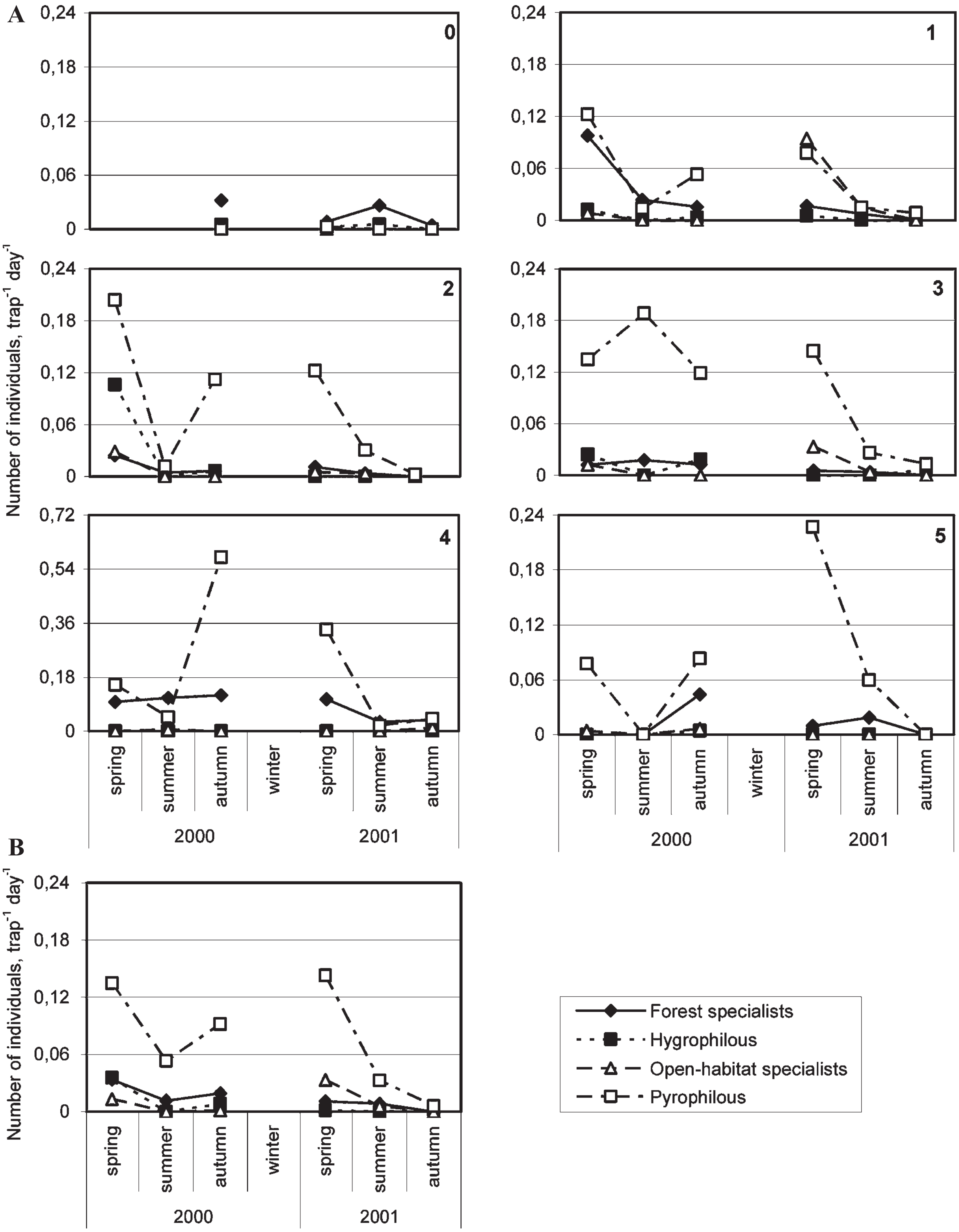

Fig. 3. Seasonal dynamics of catchability of ground beetles of four ecological groups caught during two years in all (A) studied plots and in (B) severely burned plots (mean for plots 1, 2, 3 and 5) particularly. Plot numbers are indicated in the upper right corner of the diagrams. Note a different scale at plot 4.

Рис. 3. Сезонная динамика уловистости жужелиц четырёх экологических групп, отловленных в течение двух лет (A) на всех модельных площадках и (B) только на участках пожарища (среднее для площадок 1, 2, 3 и 5). Номера площадок указаны в верхнем правом углу диаграмм. Масштаб для площадки 4 отличается от всех остальных.

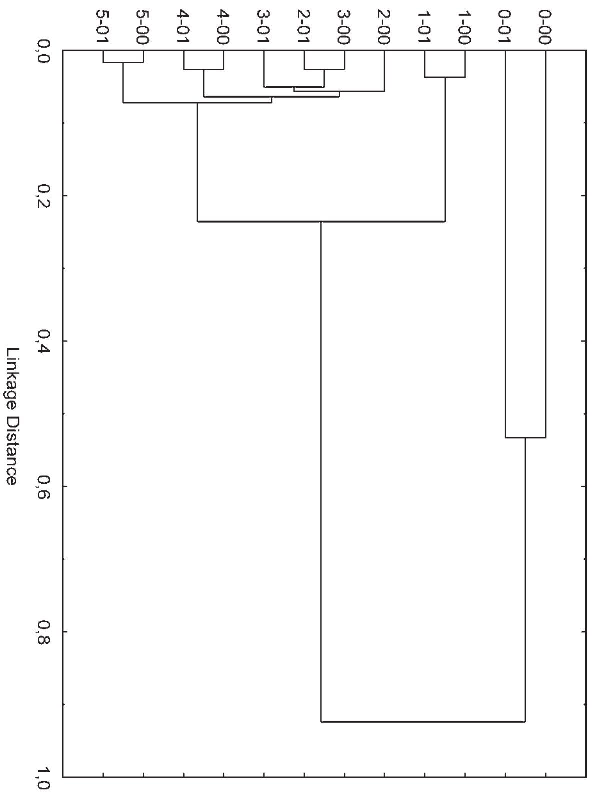

Fig. 4. Cluster diagram based on Pearson *r* similarity of 6 plots studied during 2000 and 2001.

Рис. 4. Кластер-диаграмма, рассчитанная по значениям коэффициента корреляции Пирсона (*r*) для шести площадок, исследованных в 2000-2001 гг.

dance of carabids might be that the food availability was higher. The dense, fire-killed spruce forest produced a 5–10 cm thick layer of needles on the ground at plot 4. Other taxa that served as prey to carabids and their larvae, such as Collembola and Diptera, could use this litter layer as a habitat and were caught in high densities in the pitfall traps.

This study shows that a forest fire includes remarkable variation in its effects on carabid beetles. Less severely burnt patches seemed to act as refuges for the pre-fire fauna. Because the refuges normally consisted of wet forest types, they probably only contributed to the survival of a special set of species [Gandhi et al., 2001]. The edges towards the unburnt forest contained a somewhat different assemblage of carabid beetles than the centre of the burnt area, the latter favouring the two pyrophilous species. Smaller burnt areas may in this respect represent only edges and presumably not be as favourable to pyrophilous species as large areas.

Conclusions

The study shows that a severe forest fire with regard to burning depth will favour the appearance and catchability of pyrophilous carabids in relation to other carabid species for at least two years after the burning event. Among the pyrophilous species, *Sericoda quadripunctata* was favoured by deep burning and *Pterostichus quadrifoveolatus* by weak burning. As expected, non-pyrophilous carabids survived better in weakly burnt areas than in severely burnt areas,

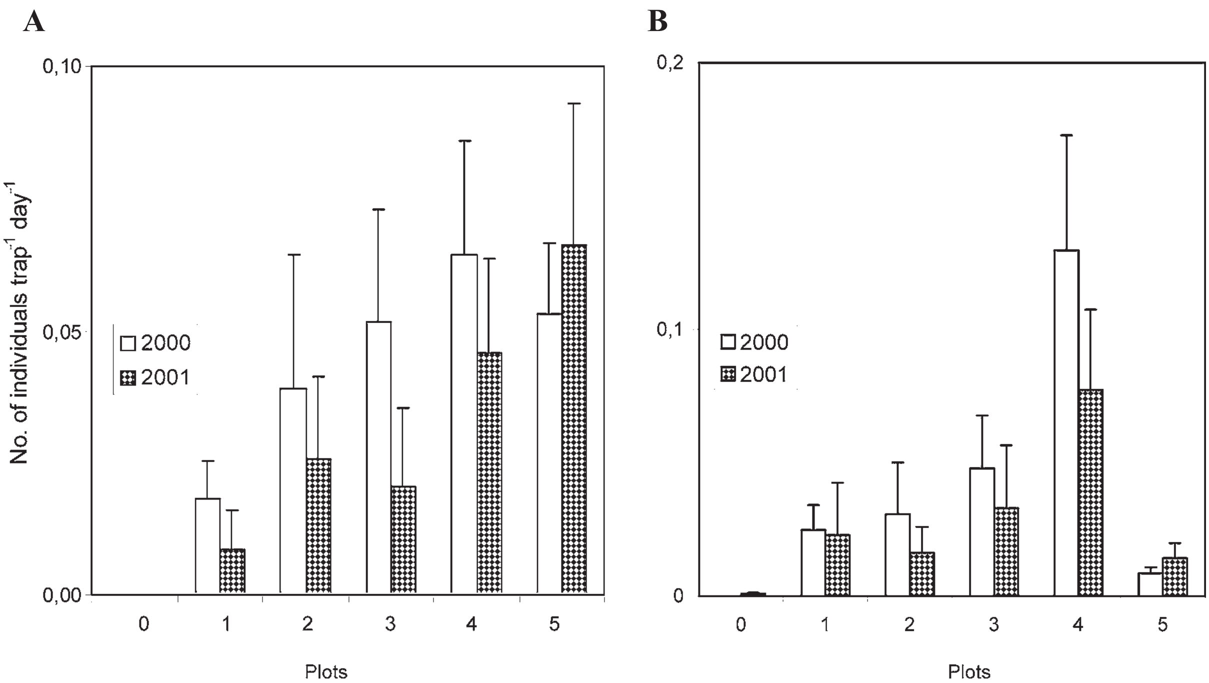

Fig. 5. Catchability of *Sericoda quadripunctata* (A) and *Pterostichus quadrifoveolatus* (B) in 2000 and 2001 (mean ± SE, n=6–10).

Рис. 5. Уловистость *Sericoda quadripunctata* (A) и *Pterostichus quadrifoveolatus* (B) в 2000 и 2001 гг. (среднее ± SE, n = 610).

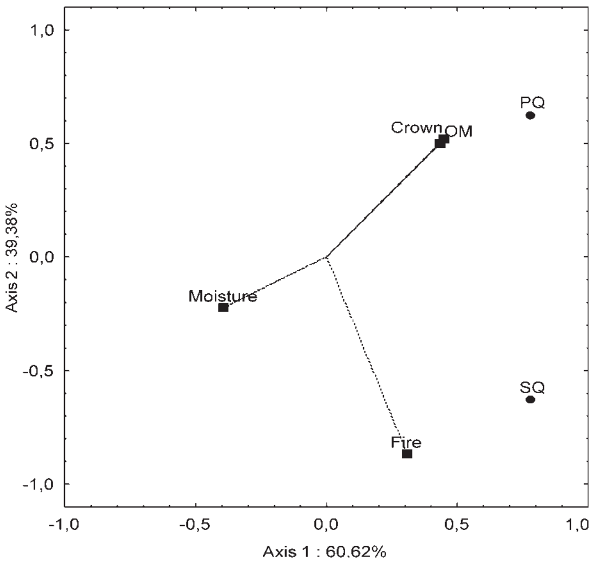

Fig. 6. CCA ordination diagram for two pyrophilous species, *Sericoda quadripunctata* (SQ) and *Pterostichus quadrifoveolatus* (PQ), and four environmental factors: fire hight (Fire), crown cover remains (Crown), organic layer remains (OM) and soil moisture (Moisture, a dummy variable). Eigenvalues: axis 1 — 1.212, axis 2 — 0.788.

Рис. 6. Диаграмма канонического анализа соответствий для двух пирофильных видов *Sericoda quadripunctata* (SQ) и *Pterostichus quadrifoveolatus* (PQ), и четырёх факторов среды — высота пламени (Fire), остаточная сомкнутость крон (Crown), остаточная органика в почве (OM) и влажность почвы (Moisture, фиктивная переменная). Характеристические числа: ось 1 — 1,212, ось 2 — 0,788.

but also in the weakly burnt areas, the pyrophilous carabids were more numerous than the non-pyrophilous carabids 1–2 years after burning. Fire severity rather than distance to the forest edge seemed to determine the population densities during the first two years after the fire.

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