ECOGRAPHY 29: 659–670, 2006

The effects of green tree retention and subsequent prescribed burning on ground beetles (Coleoptera: Carabidae) in boreal pine-dominated forests

Petri Martikainen, Jari Kouki and Osmo Heikkala

Martikainen, P., Kouki, J. and Heikkala, O. 2006. The effects of green tree retention and subsequent prescribed burning on ground beetles (Coleoptera: Carabidae) in boreal pine-dominated forests. – Ecography 29: 659–670.

We studied how two methods to promote biodiversity in managed forests, i.e. green tree retention and prescribed fire, affect the assemblages of carabid beetles. Our experiment consisted of 24 study sites, each 3–5 ha in size, which had been prepared according to factorial design. Each of the eight treatment combinations determined by the two factors explored – tree retention level (0, 10, 50 m^3 ha^{-1} and uncut controls) and prescribed use of fire (yes/no) – was replicated three times. We sampled carabids using pitfall traps one year after the treatments. Significantly more individuals were caught in most of the burned sites, but this difference was partially reflective of the trap-catches of *Pterostichus adstrictus*. The fire did not increase no. of *P. adstrictus* in the uncut sites as much as in the other sites. Species richness was significantly affected by both factors, being higher in the burned than in the unburned sites and in the harvested than in the unharvested sites. Many species were concentrated in the groups of retention trees in the burned sites, but only a few were in the unburned sites. The species turnover was greater in the burned than in the unburned sites, as indicated by the NMDS ordinations. Greater numbers of smaller sized species and proportion of brachypterous species were present in the burned sites. Fire-favored species, and also the majority of other species that prefer open habitats were more abundantly caught in the burned sites than in the unburned sites. Dead wood or logging waste around the traps did not correlate with the occurrence of species. We conclude that carabids are well adapted to disturbances, and that frequent use of prescribed fire is essential for the maintenance of natural assemblages of carabid beetles in the boreal forest. Small retention tree groups can not maintain assemblages of uncut forest, but they can be important by providing food, shelter and breeding sites for many species, particularly in the burned sites.

P. Martikainen, J. Kouki (jari.kouki@joensuu.fi) and O. Heikkala, Fac. of Forest Sciences, Univ. of Joensuu, PO Box 111, FI-80101 Joensuu, Finland.

Forest-dwelling carabid beetles have been a popular subject of various ecological studies in the northern forests particularly in Fennoscandia and Canada (Holliday 1991, 1992, Niemelä et al. 1994, Spence et al. 1996, Koivula 2001, Gandhi et al. 2001). The responses of carabid beetles to traditional forest management practices are relatively well known, particularly the effects of clearcutting, thinning, decreased age, and fragmentation of forest stands (Niemelä et al. 1988, Halme and Niemelä 1993, Heliölä et al. 2001, Koivula 2002a, Koivula et al. 2002). The results can be roughly summarized so that the more trees are removed or the smaller the remaining forest patch, the more the species assemblages change. For example, species preferring

Accepted 27 May 2006

ISSN 0906-7590

closed forest tend to decrease and open habitat species appear or increase, but generalists are not much affected (Rainio and Niemelä 2003). Small groups of retained trees in harvested areas do not seem to maintain populations of forest species (Koivula 2002a). Despite these demonstrated effects, and the suggested poor dispersal ability of some forest specialist species (Niemelä et al. 1988, Spence et al. 1996, Koivula et al. 2002), the carabid fauna of boreal forests in general seems to tolerate well the effects of forest management as it contains only few threatened species compared to many other beetle families (Gärdenfors 2000, Rassi et al. 2001).

An interesting exception are possibly formed by the carabids that are dependent on or favoured by forest fires. This group of species includes at least pyrophilous species *Pterostichus quadrifoveolatus*, *Sericoda bogemannii*, *Sericoda quadripunctata*, and also species that are less tightly associated to fires like *Bembidion grapii*, *Pterostichus adstrictus* and *Amara nigricornis* in Fennoscandia (Lundberg 1984, Muona and Rutanen 1994, Wikars 1995, Gongalsky et al. 2003). *Sericodo bogemannii* has disappeared from Fennoscandia almost completely and is critically endangered in Finland (Rassi et al. 2001) and regionally extinct in Sweden (Gärdenfors 2000). Also the more southern species, *P. quadrifoveolatus*, is vulnerable in Finland (Rassi et al. 2001). The reason for the decline of these species is apparently the lack of forest fires in the managed forest landscape. Some of these species (such as *S. quadripunctata*) may also require or at least benefit from dead trees in the burned area (Wikars 1995, 1997). Also *P. adstrictus* that is abundant in the burned forests although not confined to them, is known to utilize dead trees for ovipositing and overwintering activities (Goulet 1974). Thus, it looks evident that burned forests with plenty of dead trees may harbor carabid assemblages that differ from the unburned managed forests (Saint-Germain et al. 2005). Certain morphological and ecological attributes of the carabid assemblages may also be affected by burning e.g. Holliday (1991) found that the median body length and the percentage of brachypterous carabid species increased with time after forest fire.

In the recent years, forest management has become more biodiversity-oriented in Fennoscandia. Retention of live and dead trees at the final harvest has increased and prescribed burning of regeneration areas is also recommended although the treated areas have not increased markedly (Punttila et al. 2005). By applying green tree retention and prescribed burning together it is possible to emulate some of the effects of wildfires in managed forests and to create quickly lots of resources for species requiring charred or dead wood. However, quantitative studies to show the impacts of these widely applied measures on biodiversity in general and carabid assemblages in particular are scarce (Gandhi et al. 2004, Hyvärinen et al. 2005). In this paper we present results from a large-scale ecological experiment, where retention tree level and prescribed use of fire have been manipulated according to a factorial design. We explore how the assemblages of carabid beetles differ in burned and unburned clearcuts and forests, and how retained trees affect occurrence of species in the harvested areas. We also investigate whether environmental variables measured around the traps can explain the activity-abundance of carabid species.

Materials and methods

Study sites

This study was conducted in Lieksa, eastern Finland (63°10′N, 30°40′E), 5–35 km from the Russian border. The study area is situated on the border between southern and middle boreal zones (for a map of the area, see Hyvärinen et al. 2005). The experimental design included 24 separate study sites, 3–5 ha each, which were located within a 20×30 km area. These sites were originally ca 150 yr old forests dominated by Scots pine *Pinus sylvestris*, with Norway spruce *Picea abies* and two species of birch *Betula pendula* and *B. pubescens* as the most abundant admixed tree species. All the sites had clear signs of previous selective cuttings. However, no cuttings had taken place at the study sites during the last 50 yr before the experiment. The forests were predominantly growing on sub-xeric soils, with a variable proportion of more moist and nutrient-rich patches.

The 24 study sites were randomly allotted and subjected to different treatments according to factorial design. The factors were level of retention trees and prescribed fire (yes/no) on each site. Four tree retention levels were included: 0, 10, 50 m^3 ha^{-1} and uncut controls (Fig. 1). Retained trees were left in small circular groups, typically in three groups in 10 m^3 ha^{-1} treatment, and in five (or more) groups in 50 m^3 ha^{-1} treatment. Number of replicates in each of the eight different treatment combinations was three. The forests were harvested during the winter 2000–2001, and the 12 sites were burned on 27–28 June 2001 in similar ambient weather conditions. Details of the burning can be found from Hyvärinen et al. (2005).

There was considerable variation in the intensity of fire both within and between the sites. The mean height of flames was much lower in the uncut sites (2.2 m) than in the harvested sites (3.9 m in 50 m^3 ha^{-1} retention level and 5.8 m in 10 m^3 ha^{-1} retention level), as measured from the charred bark of the retained trees (Sidoroff 2001). Large trees survived well from the fire in the uncut sites, whereas a considerable proportion of the retention trees in the harvested sites died immediately or soon after the fire. The burning left several patches of unburned ground especially in the uncut sites. No other

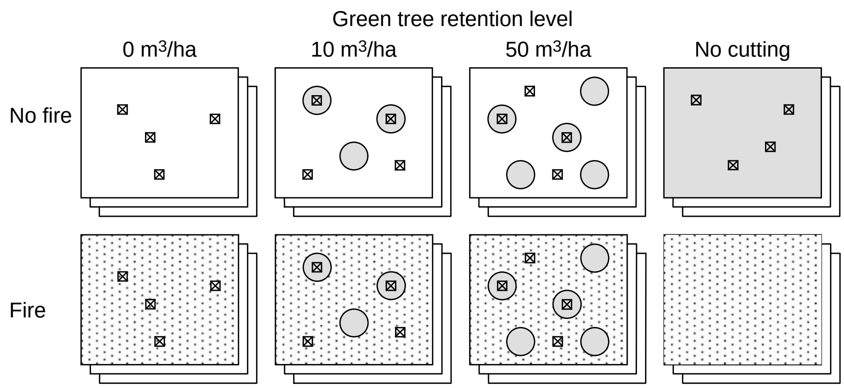

Fig. 1. Experimental design and sampling scheme. Grey areas indicate uncut parts of the stands and squares with cross indicate the location of the four groups of five pitfall traps (schematically). Number of replicates in each treatment combination was three.

active measures such as soil preparation or planting were used to enhance regeneration of the study sites during the course of this study.

Beetle sampling

The sampling of beetles started in May 2002 after all the treatments were completed. The sampling period, 13 May–12 September 2002, covered most of the growing season. Beetles were sampled using pitfall traps, consisting of 0.3 and 0.5 l plastic cups, placed within each other, and a transparent plastic roof was 20 mm above ground. The diameter of the mouth of the inner trap was 96 mm and the depth was 121 mm, and the rim was set at the level of forest floor. A solution of water, salt and detergent was used in the traps to retain and preserve fallen beetles. The traps were emptied once a month.

Four groups of five traps were installed on each site, for a total of 480 traps. In the sites with 10 and 50 m^3 ha^{-1} retention level, two of the groups were located in the open harvested area and two of the groups inside tree groups. In the clearcut sites without retained trees all traps were in open places and in uncut forests in the forest (Fig. 1). Minimum distance between groups was 20 m, and this was also the minimum distance to the nearest stand edge. The exact location of each trap-group was chosen subjectively to represent prevailing conditions of each site. The five traps in each group were placed so that four of the traps were situated in the corners of a 2 $\times$ 2 m square grid, and the fifth trap of the group in the center of the square. Samples from the five traps of each group were pooled already in the field when emptying the traps. Thus, we got four separate sub-samples (i.e. one sample per trap group) from every study site. These sub-samples were used as such, pairwise or all four sub-samples pooled, depending on the analysis in question. The carabids were identified by the author OH. Average sizes of the species and information about brachyptery were obtained from Lindroth (1985, 1986); missing data were completed from collected specimens. Eight species in the data including *Calathus micropterus*, *Carabus* spp., *Cychrus caraboides*, *Patrobus* spp. and *Trechus secalis* – were considered constantly brachypterous. Nomenclature of the carabids follows Silfverberg (2004).

Vegetation and coarse-woody debris sampling

Numbers of live and dead standing trees, logs and fresh stumps were counted from a 50 m^2 area (3.99 m radius) around the trap located in the center of each group of five traps. Percentage cover of mosses (*Sphagnum* spp. excluded, present near one trap group only), dwarf shrubs, herbs and grasses, logging residues and bare ground were estimated from a circular plot with a 12.6 m^2 area (2 m radius) around the middlemost trap (Table 1). Abundance of red wood ants (*Formica rufa* group ants) in the trap groups was registered already when the beetles were picked up from the samples using a rough, five-class scale (1: less than twenty ants per sampling period of one month; 2: less than one hundred; 3: less than one thousand; 4: less than one deciliter; 5: more than one deciliter).

Statistical analyses

Factorial analysis of variance (ANOVA) tests were used to test the effects of tree retention level and prescribed burning on the abundance, species richness, and average sizes of carabid beetles in the study sites (unit of replication: total sample of study site, thus $n = 24$). When the sizes and proportions of brachypterous species were analysed, we used Box-Cox transformation of the data if the residuals of the fitted model did not follow normal distribution. The Box-Cox parameters for the transformations that were required to normalise the errors were $\lambda = -1.4$ and $\lambda = 0$ for the sizes and proportions, respectively. The numbers of species were intentionally not standardized using rarefaction, despite

Table 1. Environmental variables included in the analyses and their abbreviations.

Abbreviation	Variable description
Variables measured from 3.99 m radius (50 m^2) around the middlemost trap	
SpruLive4	Number of living spruce trees (dbh > 5 cm)
SpruDead4	Number of standing dead spruce trees (dbh > 5 cm)
PineLive4	Number of living pine trees (dbh > 5 cm)
PineDead4	Number of standing dead pine trees (dbh > 5 cm)
DeciLive4	Number of living deciduous trees (dbh > 5 cm)
DeciDead4	Number of standing dead deciduous trees (dbh > 5 cm)
LiveTree4	Pooled number of living trees (dbh > 5 cm)
DeadTree4	Pooled number of standing dead trees (dbh > 5 cm)
Stump4	Number of fresh stumps
Log4	Number of logs (dbh > 5 cm)
BurnGround4	Proportion (%) of burned ground
Variables measured from 2 m radius around the middlemost trap	
BareGround2	Proportion (%) of ground free of vegetation, including burned surface
Moss2	Coverage (%) of mosses other than *Sphagnum*
Shrub2	Coverage (%) of dwarf shrubs
Grass2	Coverage (%) of grasses and herbs
LoggWaste2	Coverage (%) of logging residues
StumpLog2	Coverage (%) of stumps and logs
Variable derived from the traps	
Ants	Abundance of red wood ants in the traps (five-class scale)

the fact that *Pterostichus adstrictus* was very abundant in the burned harvested sites (see Discussion). The effect of retention trees on species abundance and richness was further explored in the 10 and 50 m^3 ha^{-1} harvested sites using presence of retention trees around the trap group and prescribed fire as factors in the ANOVAs (unit of replication: trap group [= five traps], thus n = 48). The ANOVAs were done with the JMP ver. 5 statistical software (Anon. 2002).

Carabid assemblages of the study sites were ordinated using non-metric multidimensional scaling (NMDS). Assemblages in retention tree groups were compared with those caught in the open parts of harvested sites or in uncut controls by performing another NMDS ordination. In this latter ordination, the sub-samples of each site were pooled pairwise, so that in the 10 and 50 m^3 ha^{-1} retention sites, the samples from tree groups were kept separated from those collected in open areas. Only species occurring in more than one site or trap pair were included, and $\log(x+1)$ transformed numbers of individuals were used in the ordinations. Sørensen distance measure was used. A two-dimensional solution was recommended for both datasets in the slow and thorough autopilot mode, and the best solutions obtained from 40 runs of NMDS with random starting configurations were stable for both datasets, as they remained essentially similar in repeated trials (Monte Carlo test, 50 randomized runs: $p = 0.0196$ for both datasets). Number of iterations for the final solution was 70 in the first and 84 in the second ordination. Ordinations were performed using 4.25 ver. of PC-ORD software (McCune and Mefford 1999).

Associations between the measured environmental variables and the abundance of individual species as well as total species number and abundance in the trap groups were assessed by Spearman rank correlations. Since the environmental variables measured around trap groups exhibited highly divergent values depending on the treatment and location of traps, the correlations were calculated for six different habitat classes separately (burned/unburned × open area/tree group/unharvested forest). Because of the high number of tests, we report only correlations having $p < 0.01$ between species and environmental variables.

Results

We collected 5770 carabid individuals belonging to 63 species (Appendix 1). *Pterostichus adstrictus* (3477 adults) alone made up 60.3% of the total catch and was very abundant in the burned harvested sites (Fig. 2a, Table 2). *Calathus micropterus* (572 adults) and *Pterostichus oblongopunctatus* (548 adults), that often dominate carabid samples in the forest, formed together 19.4% of the total sample size (Appendix 1). The share of the remaining 60 species was only 20.3%.

Of the two factors explored in the experiment, the application of fire had an effect on the number of individuals caught, but the significant interaction indicates that the effect of fire depended on the tree retention level (Table 3). The effect of retention level was almost significant, too. However, with the removal of *P. adstrictus* from the analysis there were no differences in the numbers of individuals between the treatments (Fig. 2b, Table 3) and consequently, it is likely that the effects are mostly mediated through *P. adstrictus*. The number of species caught was affected by tree retention level and burning. The number of species was clearly

Table 2. Pooled numbers of carabid individuals and species in the three sites of each treatment combination (numbers of individuals excluding *P. adstrictus* in parentheses).

Retention level	Unburned sites		Burned sites	
	No. of adults	No. of species	No. of adults	No. of species
0 m^3 ha^{-1}	361 (282)	23	1593 (279)	36
10 m^3 ha^{-1}	246 (227)	15	1564 (402)	38
50 m^3 ha^{-1}	276 (216)	24	1171 (372)	38
Uncut forest	304 (304)	10	255 (211)	13
Total	1187 (1029)	38	4583 (1264)	53

smaller in unharvested forests than in the harvested burned sites (Tukey HSD tests, Fig. 2c, Table 2).

The number of individuals per trap group was not significantly affected by trap location i.e. open areas vs tree retention groups in the 10 and 50 m^3 ha^{-1} harvested sites, but the pattern was inconsistent in different treatments (note the significant interaction between burning and trap location, Table 4). In the unburned sites, fewer individuals were caught in tree groups than in open areas, whereas an opposite pattern was found in the burned sites (Fig. 3a). The number of species caught seemed to remain somewhat lower in tree retention groups both in unburned and burned sites (Table 4, Fig. 3b).

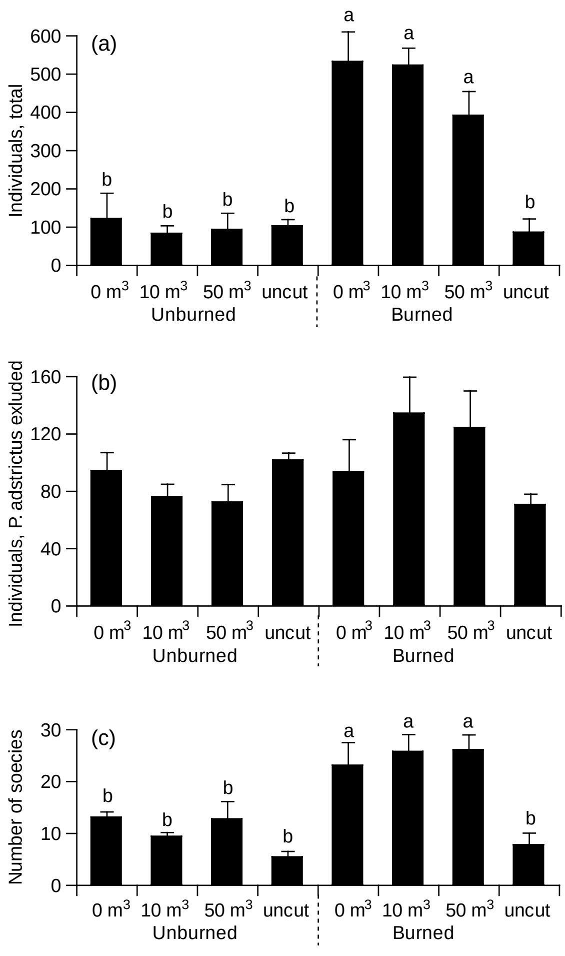

Fig. 2. (a) Number of carabid individuals caught in each of the study sites. (b) Number of individuals exluding *Pterostichus adstrictus* in the corresponding samples. (c) Number of species caught in each of the study sites. Data are means +SE. Treatment combinations not connected by same letter are significantly different (Tukey HSD test, in Fig. 2b no pairwise differences were found).

The two-dimensional NMDS-ordination based on the pooled samples of each study site showed that the carabid assemblages in the burned harvested sites clearly differed from the other sites, including from that of the burned uncut forests (Fig. 4). Also most of the species were associated with the burned harvested sites (Fig. 5). Another NMDS-ordination was performed so that the samples from the trap groups of each study site were pooled pairwise, keeping the samples from open places and groups of retained trees separately in the 10 and 50 m^3 ha^{-1} retention sites. This ordination showed that carabid assemblages in the groups of retained trees were intermediate to those collected from clearcuts or treeless parts of harvested sites and unharvested forests (Fig. 6).

The coverage of mosses and dwarf shrubs increased to bottom-right in the latter ordination (Fig. 6) and coverage of soil without any vegetation increased in the opposite direction where the samples from burned sites were located. Another gradient was related to the abundance of red wood ants, which increased to top-right. Density of living trees increased to the right in the ordination, and coverage of cut stumps and logs increased in the opposite direction. The correlations were essentially similar in the ordination based on pooled samples (not shown; Fig. 4). Variables related to dead trees were only weakly correlated with axes 1 and 2 in the ordination space.

Twenty-six species were represented with >10 individuals in the data, and were further investigated for their habitat associations. These species were classified into four groups with different habitat associations in our data (Appendix 1). Four of the species, i.e. *Calathus micropterus*, *Notiophilus biguttatus*, *Carabus glabratus* and *Cychrus caraboides*, were rather clearly associated with unharvested forests. Two species, *Pterostichus oblongopunctatus* and *Notiophilus palustris*, demonstrated indifferent response to forest cover. All the remaining twenty species were almost exclusively caught in the harvested sites, or exhibited strong association with burned sites (*Notiophilus germinyi* and *Bembidion*

Table 3. Two-way ANOVA results for the total number of individuals (with and without *P. adstrictus*) and species caught per study site in the different treatment combinations. Based on log(x+1) transformed numbers of individuals and species. TRL = tree retention level.

	Source	DF	MS	F	P-value
Total number of individuals	TRL	3	0.234	3.203	0.052
	Burning	1	1.681	23.022	0.000
	TRL × burning	3	0.344	4.708	0.015
	Error	16	0.073		
Individuals, *P. adstrictus* excluded	TRL	3	0.013	0.165	0.918
	Burning	1	0.055	0.691	0.418
	TRL × burning	3	0.095	1.202	0.341
	Error	16	0.079		
Total number of species	TRL	3	0.251	11.493	0.000
	Burning	1	0.421	19.313	0.000
	TRL × burning	3	0.024	1.120	0.370
	Error	16	0.022		

grapii). Only four of the 20 species associated with open habitats did not favour burned sites.

The 37 rare species (< 10 adults) showed similar proportions in their habitat associations as did the more abundant species (Appendix 1). Taking into account the numbers of individuals of each species (but not the total sample sizes), and that only 20% of the traps were located in uncut forests, 14.2 (38%) of these 37 rare species should have been caught in the uncut sites. However, only seven species (19%) were detected there. Also the number of rare species caught in unburned sites, eighteen, was smaller than the expected value of 25.7.

The species showed strikingly different associations with retention tree groups in burned and unburned sites (Appendix 1). Only three species (*Carabus glabratus*, *Amara brunnea* and *Notiophilus reitteri*) were more numerous in the traps located within tree groups than in open areas in the unburned 10 and 50 m^3 ha^{-1} retention sites. In the burned areas, 20 species out of 48 (e.g. *Notiophilus aquaticus*, *N. biguttatus*, *N. germinyi*, *Bembidion grapii* and *Sericoda quadripunctata*) were more abundantly caught in the tree groups.

One group of traps in the whole study was placed in a moist, *Sphagnum*-dominated surface. This single group of five traps, located within open area in an unburned 50 m^3 ha^{-1} site, produced at least 40% of individuals of *Agonum fuliginosum* (eight of the altogether 12 individuals), *Amara plebeja* (1/1), *Patrobus assimilis* (3/5), *Platynus mannerheimii* (1/2), *Pterostichus nigrita* (3/5), and *Pterostichus rhaeticus* (4/10).

The average size of species was significantly smaller in the burned than in the unburned sites (Fig. 7a, Table 5). The percentage of brachypterous species was significantly higher in the unburned than in the burned sites, and also tree retention level had a significant effect so that in the uncut areas their proportion was higher than in other retention levels (Fig. 7b, Table 5, Tukey HSD). Interaction between the treatment factors did not significantly modify the occurrence of the brachypterous species (Fig. 7b, Table 5).

A few strong correlations were detected between environmental variables and species (Table 6). However, after plotting the data and considering the high number of tests made, most of them were suspected to represent Type I errors (p-values were deliberately not Bonferroni adjusted; see also comments in Table 6). In the unburned sites, ants always had positive correlation with *Calathus micropterus* and negative correlation with *Carabus glabratus*, *Pterostichus oblongopunctatus* and *Cychrus caraboides*, although all the correlations were not significant. Other environmental variables showed only very few plausible correlations with the abundance of individual species (Table 6, Fig. 8a, b). Total number of individuals caught per trap group was not strongly correlated with any of the variables tested, whereas the number of species showed strong negative

Table 4. Two-way ANOVA results for numbers of individuals and species per trap group in the open areas and retention tree groups in the 10 and 50 m^3 ha^{-1} harvested sites. Numbers of individuals are log(x+1) transformed.

	Source	DF	MS	F	Sig.
Total number of individuals	Burning	1	7.231	111.671	0.000
	Trap location	1	0.045	0.697	0.408
	Burning × trap location	1	0.409	6.315	0.016
	Error	44			
Total number of species	Burning	1	744.188	86.989	0.000
	Trap location	1	35.021	4.094	0.049
	Burning × trap location	1	15.188	1.775	0.190
	Error	44			

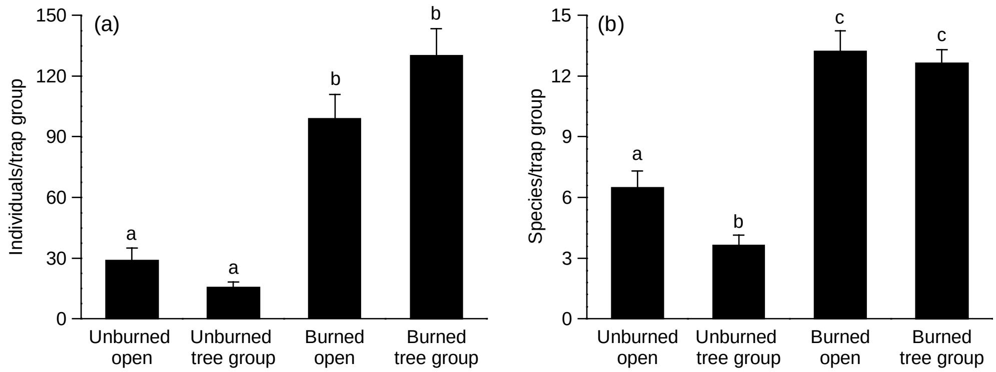

Fig. 3. Average numbers (+SE) of individuals (a) and species (b) per trap group located either in the open parts or inside retention tree groups in the 10 and 50 m^3 ha^{-1} harvested sites.

correlation with ants in three out of six habitat classes (Table 6).

Discussion

Our results confirmed that carabid assemblages are fundamentally affected by both green tree retention and prescribed fire. However, quantifying this change was somewhat problematic, because one species, *Pterostichus adstrictus*, was very abundant and strongly dominated the samples in the burned harvested sites and made up 75.6% of the total catch there. The corresponding figure was only 17.9% in the unburned harvested sites, and even smaller in the uncut sites. The interpretation of our results is consequently rather different depending on the way how this species is taken into account in the analyses. One alternative is to assume that the variation in the sample sizes is mainly a result of different efficiency of the traps, caused by variable beetle activity, and amount of ground vegetation impeding movement, in the different treatments (Greenslade 1964). This would, however, lead to a rather unreasonable assumption that our traps were four to six times more effective in burned harvested sites than in corresponding unburned sites, but actually less effective in burned than in unburned forests. In such a situation, standardization of samples into equal sample sizes using rarefaction or related methods would in practice mean that we assume that species other than *P. adstrictus* were ca three times more abundant in the unburned than in the burned harvested sites, although their true catches did not differ between the treatments. Another alternative is to assume that the traps are roughly equally effective in unburned and burned habitats and that the catches reflect real differences in the species' abundances among the sites. Following this alternative we would end up in a result that *P. adstrictus* was 21 times more abundant in the burned than in the unburned sites, but the pooled abundance of other species did not differ between the treatments. This alternative seems more plausible, as *P. adstrictus* is a fire-favored species and it has also previously been observed to increase considerably in number after prescribed fire (Holliday 1992, Muona and Rutanen 1994, Wikars 1997). Thus, we found it justified to follow the latter alternative and did not use rarefaction in the analyses, although we acknowledge that the efficiency of the traps probably varied among the treatments to some extent.

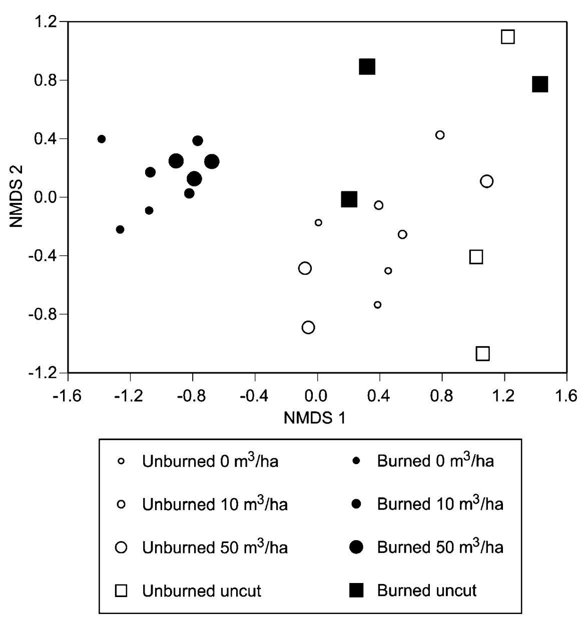

Fig. 4. The two-dimensional solution of the NMDS-ordination of the study sites. Proportion of variance represented by axis 1 is 70.8% and that of axis 2 19.3%.

It is expected that the species richness of carabids would increase after harvesting, as specialists of open habitats are known to colonize these areas (Heliölä et al. 2001, Koivula 2002a, Huber and Baumgarten 2005). Similar to our results, the colonists arriving at a forest after a disturbance, such as clearcutting (Huber and

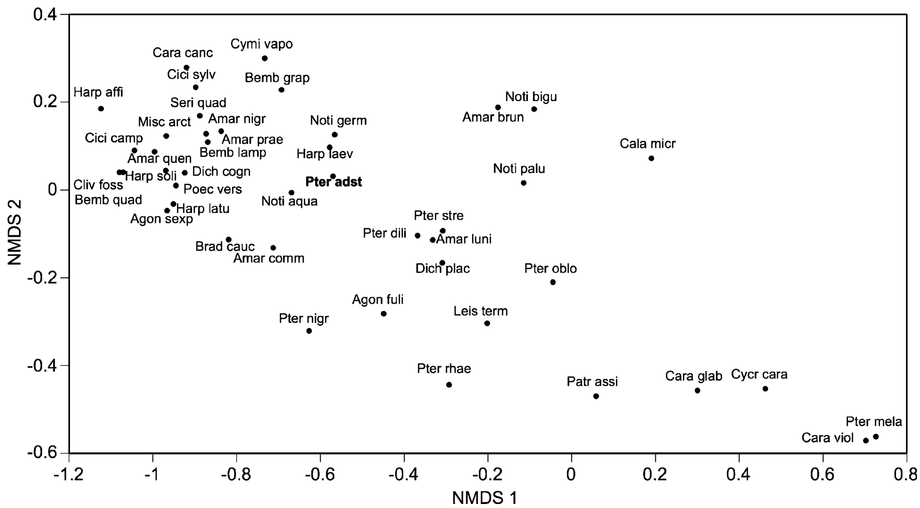

Fig. 5. Location of individual species in the NMDS-ordination of the study sites.

Baumgarten 2005) and forest fire (Holliday 1991), have been observed to be smaller and to contain proportionally more macropterous species compared with the predisturbance assemblages. In our study, both the smaller size of species and smaller proportion of brachypterous species in the burned than in the unburned sites suggest that species turnover was greater in the burned sites. Large-bodied brachypterous species like *Carabus glabratus* and *Cychrus caraboides* may suffer from fire more than smaller species do, and are not as rapid in recolonizing the areas due to limited dispersal ability. Fire may also decrease the availability of their important food items, slugs, which are sensitive to drought. *Carabus glabratus* and *C. caraboides* were indeed clearly less abundant in the burned than in the unburned sites. The size of species and proportion of brachypterous species can be expected to increase with time in the burned sites, as reported by Holliday (1991) in Canada.

It was also interesting that not only those species that are known to favor burned areas (such as *Sericoda quadripunctata* and *Bembidion grapii*), but also the majority of other species that prefer open habitats were clearly more abundant in the burned than in the unburned sites. The beetle assemblages of burned harvested sites were thus distinct from those of unburned sites, and contained several species that were scarce or absent in the unburned sites. On the other hand, only one abundant species, *Cychrus caraboides*, was almost absent from the burned sites. *Cychrus caraboides* is one of the few carabid species possibly associated with old forests, although it is frequently reported from harvested stands as well (Niemelä et al. 1988, Heliölä et al. 2001, Koivula 2002a, Koivula et al. 2002). Furthermore, none of the species with more than one individual was confined to the uncut sites. This observation is in agreement with several earlier studies conducted in the boreal forests of Europe (Niemelä et al. 1996, Heliölä et al. 2001, Koivula 2002b) and Canada (Gandhi et al. 2004).

Retention tree patches must apparently be considerably larger than in our study, perhaps up to 1–2 ha, to effectively retain characteristics of mature forest important for carabid beetles, and even then it would be questionable whether they could act as stand analogues of true fire residuals (Gandhi et al. 2001, 2004). The species assemblages observed in the retention tree groups in our data were intermediate to those in open areas of harvested sites and uncut forests, but the species showed different responses to the tree groups depending on the environment as in the unburned sites tree groups were not particularly favored, whereas the opposite was true in the burned sites. Even the forest species seemed to follow this pattern. One explanation is that in the burned areas where fire has destroyed the lower vegetation and logging slash almost completely, the retention tree groups may be the only places where beetles can find shade and shelter. In the unburned harvested sites there is abundant vegetation and logging slash throughout the area, and consequently, beetles do not concentrate in residuals. It is also possible that food-availability is enhanced in the burned retention tree patches as the fire-damaged trees shed their needles and leaves still green, forming nutrient-rich litter that support saprophagous invertebrates such as springtails (Collembola).

Some carabids, particularly *Dromius* spp., are confined to trees (Lindroth 1986), and could be expected to benefit from retention trees in harvested areas. The whole genus *Dromius* was however totally missing from our material, apparently due to the sampling method. *Sericoda quadripunctata* is another example of species that is often found under the bark of trees (Lindroth 1986), and has been observed to prefer burned uncut forests over burned clearcuts (Wikars 1995). However, in our study it was most abundantly caught in the retention tree groups of burned harvested sites and not at all recorded in the uncut forests. A few other abundant species such as *Notiophilus aquaticus*, *N. biguttatus*,

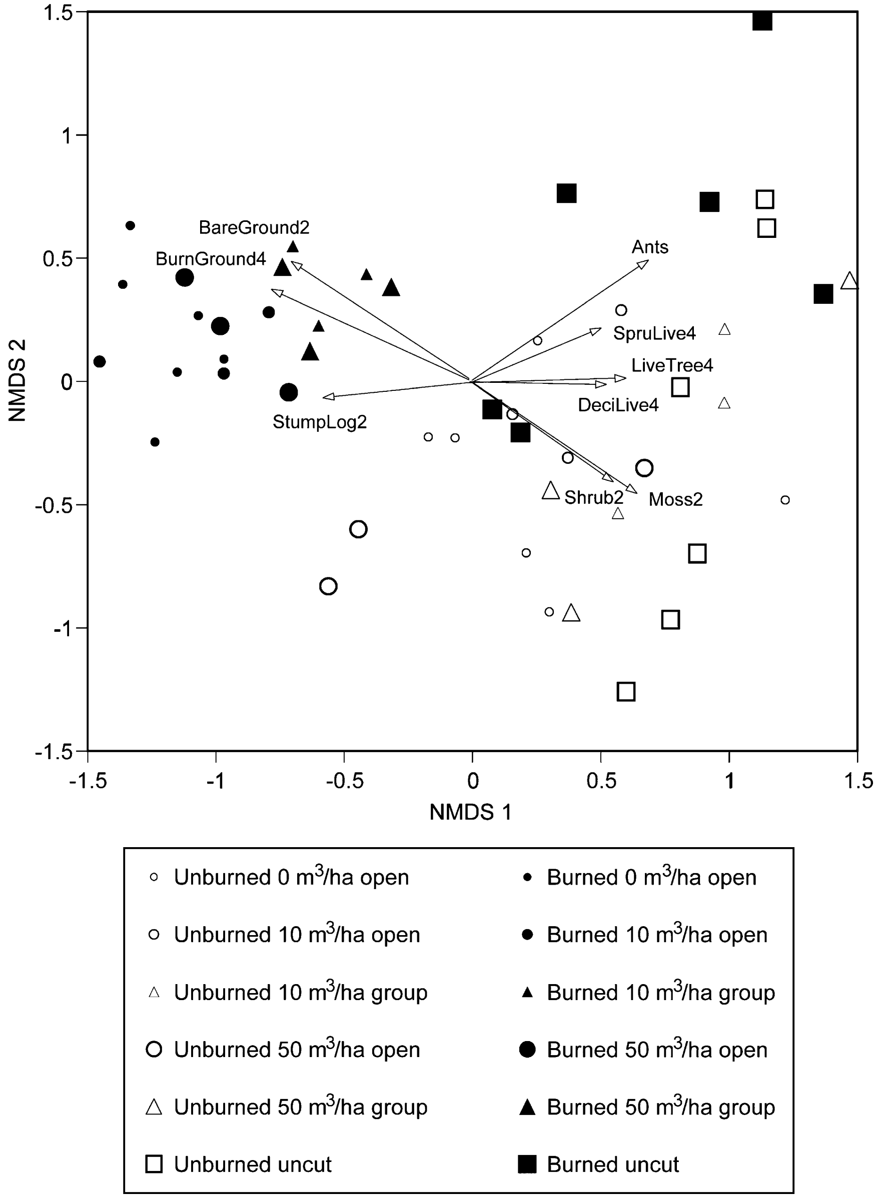

Fig. 6. NMDS-ordination of the pooled samples of two trap groups in each site, showing samples from the groups of retained trees separately from those collected in the open areas of corresponding study sites. Proportion of variance represented by axis 1 is 66.6% and that of axis 2 20.0%. Environmental variables (Table 1) having strong correlations ($r^2 \geq 0.25$) with either of the axes are presented as arrows.

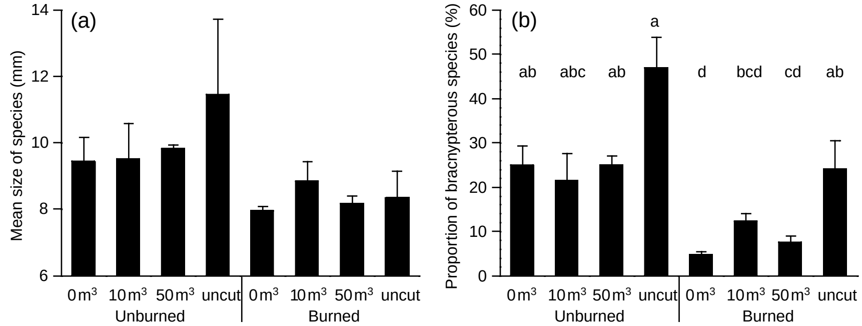

Fig. 7. Average (+SE) size of species (a) and the proportion of brachypterous species (b) in the different treatments. All species were given equal weight regardless of the relative abundance in each site. Treatment combinations not connected by same letter are significantly different (Tukey HSD test, in (a) no pairwise differences were found).

Table 5. Two-way ANOVA results for the size of species and proportion of brachypterous species per site in the different treatment combinations. Based on Box-Cox transformed data. TRL = tree retention level.

	Source	DF	MS	F	Sig.
Size of individuals	TRL	3	0.269	0.104	0.956
	Burning	1	11.620	4.501	0.0498
	TRL × burning	3	0.606	0.235	0.871
	Error	16	2.582		
Proportion of brachypterous species	TRL	3	348.831	10.067	0.001
	Burning	1	1679.736	48.477	0.000
	TRL × burning	3	106.270	3.067	0.058
	Error	16	34.650		

N. germinyi and *Bembidion grapii* that were confined to burned areas were also associated with residuals in the burned harvested sites, although these species are not known to depend on the presence of trees. *Notiophilus* spp. and *S. quadripunctata* feed on Collembola (Lindroth 1985, 1986), which may explain their affinity to tree groups in the burned sites.

The ordinations showed that some of the environmental variables measured around the trap groups were correlated with the carabid assemblages. These variables included ground-layer characteristics, living trees, and abundance of red wood ants. Correlations were also detected between individual species and environmental variables, e.g. *Calathus micropterus* had positive correlations with red wood ants in unburned sites and a negative correlation with bare ground in burned harvested sites. These findings agree well with earlier observations (Niemelä et al. 1992, Koivula and Niemelä 2003). Standing or downed dead trees did not correlate with the species composition or occurrence of individual species. It has been suggested that logging residue might have a positive impact on ground-active beetles (Gunnarsson et al. 2004), but we did not find such an effect on carabids. Nevertheless, the number of cut

Table 6. Significant Spearman correlations ($p < 0.01$) detected between the abundance of individual species and total species number, and environmental variables (see Table 1) in the trap groups located in different kinds of treatments. Only species occurring in >33.4% of the trap groups in each habitat class were tested to avoid the influence of zeros to the analyses. Thus, we essentially restricted the analyses only to species that were relatively constantly occurring in the study sites.

Treatments	Species	Environmental variable	N of trap groups	r_s	P	Comments
Unburned harvested, open areas	*Pterostichus adstrictus*	Stump4	24	0.547	0.006	a
Unburned harvested, tree groups	*Calathus micropterus*	Ants	12	0.756	0.004	a
	Carabus glabratus	Ants	12	−0.739	0.006	ab
	Pterostichus oblongopunctatus	Ants	12	−0.720	0.008	a
	Species total	Ants	12	−0.790	0.002	a
Unburned, uncut	*Calathus micropterus*	SpruLive4	12	0.818	0.001	cd
	Calathus micropterus	LiveTree4	12	0.724	0.008	cd
	Calathus micropterus	Ants	12	0.763	0.004	acd
	Carabus glabratus	SpruLive4	12	−0.722	0.008	bcd
	Carabus glabratus	Ants	12	−0.778	0.003	abcd
	Cychrus caraboides	SpruLive4	12	−0.812	0.001	bcd
	Cychrus caraboides	LiveTree4	12	−0.715	0.009	bcd
	Cychrus caraboides	Ants	12	−0.857	0.003	abcd
	Notiophilus biguttatus	DeadTree4	12	0.724	0.008	bce
	Species total	Ants	12	−0.754	0.005	acd
	Species total	SpruLive4	12	−0.749	0.005	cd
Burned harvested, open areas	*Amara nigricornis*	Stump4	24	−0.711	<0.001	b
	Amara praetermissa	Stump4	24	−0.682	<0.001	b
	Harpalus laevipes	BurnGround4	24	−0.516	0.010	e
	Pterostichus strenuus	LoggWaste2	24	0.649	0.001	b
	Species total	Stump4	24	−0.576	0.003	c
Burned harvested, tree groups	*Calathus micropterus*	BareGround2	12	−0.931	<0.001	ae
	Notiophilus aquaticus	Ants	12	0.806	0.002	be
	Sericoda quadripunctata	BurnGround4	12	−0.727	0.007	e
Burned, uncut	Species total	Ants	12	−0.767	0.004	ac

[a]A pattern that can be supported by the biology of the species.
[b]High proportion of zero-catches.
[c]High influence of deviating individual study site(s), risk of pseudoreplication.
[d]Ants, SpruLive4 and LiveTree4 strongly intercorrelated.
[e]Very short environmental gradient.

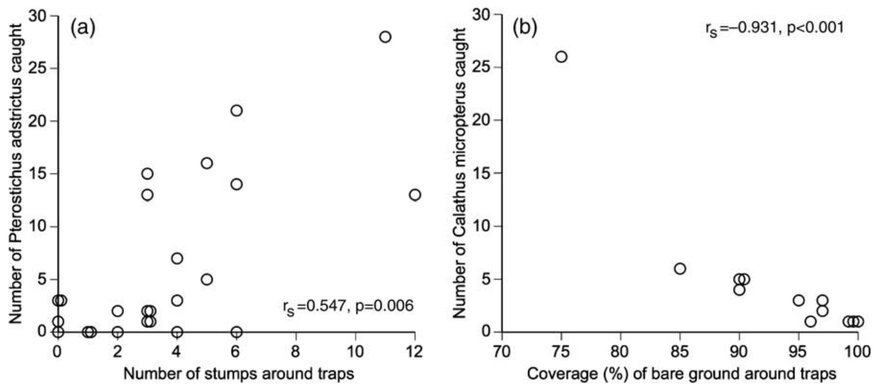

Fig. 8. Scatterplots showing (a) the relationship between number of stumps around (r = 4 m) and number of *Pterostichus adstrictus* caught per trap group in the open parts of unburned sites, and (b) the relationship between coverage of ground free of vegetation around (r = 2 m) and number of *Calathus micropterus* individuals caught per trap group in tree groups in burned harvested sites.

stumps around the traps seemed to affect the abundance of *Pterostichus adstrictus* in the open parts of unburned harvested sites. This species is often found under the bark and the females are known to oviposit in dead wood (Goulet 1974), which may explain our observation.

Conclusions

The scarcity of carabid species confined to uncut forests on one hand, and the presence of many species in burned areas on other hand suggest that boreal forest carabids are in general well adapted to frequent disturbance caused by forest fire. Since many species, including a threatened one *Pterostichus quadrifoveolatus*, were predominantly found in the burned sites, we can conclude that successful maintenance of natural carabid communities in the boreal forest requires the use of prescribed fire in forest management (see also Gandhi et al. 2001, 2004). This is further stressed by the fact that the only boreal forest carabids classified as threatened in Finland are those associated with burned forests. The use of prescribed fire in forest management is beneficial for many other coleopteran species (Hyvärinen et al. 2005).

Retention tree groups of the size used in our study were apparently far too small to maintain properties of uncut forest important for carabids (see also Koivula 2002a). Nevertheless, they can have an important role particularly in burned harvested areas by providing food and shelter for a number of ground-dwelling species and by being breeding sites for species like *Sericoda quadripunctata* that are associated with dead trees. The significance of retention trees for saproxylic species (i.e. species dependent on dead trees) is greater in many insect groups, making tree retention in harvest operations more justified (Martikainen 2001, Kouki et al. 2001, Sverdrup-Thygeson and Ims 2002).

The role of variables related to dead wood or logging residue on carabid occurrence was negligible, which is understandable as most carabids do not require these resources. Thus, the use of carabids as indicators of biodiversity of other species groups is probably largely limited to other ground arthropods, and should not be extended to other forest species groups, such as those dependent upon dead wood or threatened species.

Acknowledgements – We thank Metsähallitus (Finnish Forest and Park Service) for co-operation and practical support in providing forests for the study and executing the experimental treatments. We are grateful to Markku Karttunen and Harri Lappalainen for help in the field and in the identification of specimens; Matti Koivula for help with the literature; Pekka Punttila, and Esko Hyvärinen for valuable comments on the manuscript. This study was funded by the Academy of Finland (64308, 111941), Finnish Forest and Park Service, Finnish Forest Industries Association and the Ministries of Environment and Agriculture and Forestry (all grants to author JK).

References

Anon. 2002. JMP® version 5. Statistics and graphics guide. – SAS Inst.

Gandhi, K. et al. 2001. Fire residuals as habitat reserves for epigaeic beetles (Coleoptera: Carabidae and Staphylinidae). – Biol. Conserv. 102: 131–141.

Gandhi, K. et al. 2004. Harvest retention patches are insufficient as stand analogues of fire residuals for litter-dwelling beetles in northern coniferous forests. – Can. J. For. Res. 34: 1319–1331.

Gärdenfors, U. (ed.) 2000. Red list of Swedish species. – ArtDatabanken, SLU.

Gongalsky, K. B. et al. 2003. Dynamics of pyrophilous carabids in a burned pine forest in central Sweden. – Baltic J. Coleopterol. 3: 107–111.

Goulet, H. 1974. Biology and relationships of *Pterostichus adstrictus* Eschscholtz and *Pterostichus pensylvanicus* Leconte (Coleoptera: Carabidae). – Quaest. Entomol. 10: 3–33.

Greenslade, P. M. J. 1964. Pitfall trapping as a method for studying populations of Carabidae (Coleoptera). – J. Anim. Ecol. 33: 301–310.

Gunnarsson, B. et al. 2004. Effects of logging residue removal on ground-active beetles in temperate forests. – For. Ecol. Manage. 201: 229–239.

Halme, E. and Niemelä, J. 1993. Carabid beetles in fragments of coniferous forest. – Ann. Zool. Fenn. 30: 17–30.

Heliölä, J. et al. 2001. Distribution of carabid beetles (Coleoptera, Carabidae) across a boreal forest-clearcut ecotone. – Conserv. Biol. 15: 370–377.
Holliday, N. 1991. Species responses of carabid beetles (Coleoptera: Carabidae) during post-fire regeneration of boreal forest. – Can. Entomol. 123: 1369–1389.
Holliday, N. 1992. The carabid fauna (Coleoptera: Carabidae) during postfire regeneration of boreal forest: properties and dynamics of species assemblages. – Can. J. Zool. 70: 440–452.
Huber, C. and Baumgarten, M. 2005. Early effects of forest regeneration with selective and small scale clear-cutting on ground beetles (Coleoptera, Carabidae) in a Norway spruce stand in southern Bavaria. – Biodiv. Conserv. 14: 1989–2007.
Hyvärinen, E. et al. 2005. Short-term effects of controlled burning and green-tree retention on beetle (Coleoptera) assemblages in managed boreal forests. – For. Ecol. Manage. 212: 315–332.
Koivula, M. 2001. Carabid beetles (Coleoptera, Carabidae) in boreal managed forests-meso-scale ecological patterns in relation to modern forestry. – Ph.D. thesis, Dept of Ecology and Systematics, Div. of Population Biology, Univ. of Helsinki.
Koivula, M. 2002a. Alternative harvesting methods and boreal carabid beetles (Coleoptera, Carabidae). – For. Ecol. Manage. 167: 103–121.
Koivula, M. 2002b. Boreal carabid-beetle (Coleoptera, Carabidae) assemblages in thinned uneven-aged and clear-cut spruce stands. – Ann. Zool. Fenn. 39: 131–149.
Koivula, M. and Niemelä, J. 2003. Gap felling as a forest harvesting method in boreal forests: responses of carabid beetles (Coleoptera, Carabidae). – Ecography 26: 179–187.
Koivula, M. et al. 2002. Boreal carabid-beetle (Coleoptera, Carabidae) assemblages along the clear-cut originated succession gradient. – Biodiv. Conserv. 11: 1269–1288.
Kouki, J. et al. 2001. Forest fragmentation in Fennoscandia: linking habitat requirements of wood-associated threatened species to landscape and habitat changes. – Scand. J. For. Res. Suppl. 3: 27–37.
Lindroth, C. H. 1985. The Carabidae (Coleoptera) of Fennoscandia and Denmark. – Fauna Entomol. Scand. 15: 1–225.
Lindroth, C. H. 1986. The Carabidae (Coleoptera) of Fennoscandia and Denmark. – Fauna Entomol. Scand. 15: 233–497.
Lundberg, S. 1984. The beetle fauna of burnt forest in Sweden. – Entomol. Tidskr. 105: 129–141, in Swedish.
Martikainen, P. 2001. Conservation of threatened saproxylic beetles: significance of retained aspen *Populus tremula* on clearcut areas. – Ecol. Bull. 49: 205–218.
McCune, B. and Mefford, M. J. 1999. PC-ORD. Multivariate analysis of ecological data. – MjM Software.
Muona, J. and Rutanen, I. 1994. The short-term impact of fire on the beetle fauna in boreal coniferous forest. – Ann. Zool. Fenn. 31: 109–121.
Niemelä, J. et al. 1988. The distribution of carabid beetles in fragments of old coniferous taiga and adjacent managed forest. – Ann. Zool. Fenn. 25: 107–119.
Niemelä, J. et al. 1992. Small-scale heterogeneity in the spatial distribution of carabid beetles in the southern Finnish taiga. – J. Biogeogr. 19: 173–181.
Niemelä, J. et al. 1994. Patterns of carabid diversity in Finnish mature taiga. – Ann. Zool. Fenn. 31: 123–129.
Niemelä, J. et al. 1996. The importance of small-scale heterogeneity in boreal forests: variation in diversity in forest-floor invertebrates across the succession gradient. – Ecography 19: 352–368.
Punttila, P. et al. 2005. 3.2. Metsät. – In: Hildén, M. et al. (eds), Evaluation of the Finnish national action plan for biodiversity. Suomen ympäristö, pp. 37–51, in Finnish.
Rainio, J. and Niemelä, J. 2003. Ground beetles (Coleoptera: Carabidae) as bioindicators. – Biodiv. Conserv. 12: 487–506.
Rassi, P. et al. (eds) 2001. Threatened species in Finland in 2000. – Ministry of the Environment and Finnish Environment Inst., in Finnish.
Saint-Germain, M. et al. 2005. Short-term response of ground beetles (Coleoptera: Carabidae) to fire and logging in a spruce-dominated boreal landscape. – For. Ecol. Manage. 212: 118–126.
Sidoroff, K. 2001. Metsäpalon vaikutus puuston kuolleisuuteen ja lahopuun määrään, kokeellinen tutkimus Lieksassa. – M.Sc. thesis, Univ. of Joensuu, Finland.
Silfverberg, H. 2004. Enumeratio nova Coleopterorum Fennoscandiae, Daniae et Baltiae. – Sahlbergia 9: 1–111.
Spence, J. et al. 1996. Northern forestry and carabids: the case for concern about old-growth species. – Ann. Zool. Fenn. 33: 173–184.
Sverdrup-Thygeson, A. and Ims, R. A. 2002. The effect of forest clearcutting in Norway on the community of saproxylic beetles on aspen. – Biol. Conserv. 106: 347–357.
Wikars, L.-O. 1995. Clear-cutting before burning prevents establishment of the fire-adapted *Agonum quadripunctatum* (Coleoptera: Carabidae). – Ann. Zool. Fenn. 32: 375–384.
Wikars, L.-O. 1997. Pyrophilous insects in Orsa Finnmark, central Sweden: biology, distribution, and conservation. – Entomol Tidskr. 118: 155–169, in Swedish.

Download the appendix as file E4562 from <www.oikos.ekol.lu.se/appendix>.

Subject Editor: John Spence.