

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 (Höglwald)

CHRISTIAN HUBER* and MANUELA BAUMGARTEN

*Fachgebiet für Waldernährung und Wasserhaushalt, Department für Ökologie, Wissenschaftszentrum Weihenstephan, TU-München, Am Hochanger 13, D-85354 Freising, Germany; *Author for correspondence (e-mail: Huber@forst.tu-muenchen.de; phone: +49-8161-714789; fax: +49-8161-714738)*

Received 25 August 2003; accepted in revised form 27 February 2004

Key words: Carabidae, Clear-cutting, Diversity, Forest management, Selective-cutting, Species richness, Species-environment relationship, Spruce

Abstract. This study investigates the early effects of forest regeneration with selective, and small scale clear-cutting, on ground beetle (Coleoptera, Carabidae) community composition in a homogenous, mature spruce forest in Southern Bavaria (Höglwald), Germany. Carabid beetles were sampled with pitfall-, emergence-, and window-traps, from 1999 to 2001 during a pre-treatment year, the year of cutting, and the year after cutting. In the spruce stand we found a relatively low species richness with few dominating species. Selective cutting preserved this carabid assemblage. At the clear-cuts carabid species richness increased in the year of cutting, because of the invasion of small open field species, and the persistence of most forest species. Also, number of individuals increased due to higher numbers caught in the window-traps. The first open habitat species appeared just a few months after felling. However, in the next year the numbers of individuals, especially of forest species, were drastically reduced. Also, the number of species decreased, and was just slightly higher than on the control plot (mature stand). According to the DCA (detrended correspondence analysis) forest interior species had the same habitat preferences as net building spiders (Amaurobiidae, Linyphiidae) and other families of beetles (Staphylinidae, Curculionidae). Several groups of open habitat species responded positively on different patches found in the clear-cut: (1) diversity of ground vegetation, respectively coverage of shrubs, (2) favour for moist patterns, and water filled ruts (together with Gastropoda), or (3) low coverage of ground vegetation (together with free hunting spiders, Lycosidae). Different structures side by side (mature forest, selective cutting, open areas) may improve diversity on a forest scale. Small openings can serve as an important retreat for open habitat species. However, if clear-cuts become the dominant element, forest species may be threatened. With selective cutting species richness of carabids is not improved; however, the remaining forest carabid species may be preserved during the early phase of the regeneration process.

Introduction

Today a main task of forest management is to maintain sustainability, including wood production, and non-timber values (United Nations 1992; Lindenmayer et al. 2000). In the past, European beech forests have been replaced in wide areas of southern Germany by managed evenly-aged Norway

spruce forests. Norway spruce is now the dominating species in this region. These spruce stands are well known to foresters for their high productivity (Röhle 1991; Pretzsch 1996). However, concern is rising about possible negative ecological impacts. These evenly-aged spruce stands are highly susceptible to frequent storm events and insect outbreaks (Rothe and Borchert 2003). Soil acidification (Kreutzer 1995), nitrate contamination of groundwater resources (Rothe et al. 2002), and unexpected high N₂O emissions from the soils (Butterbach-Bahl et al. 1998), are serious problems especially in areas with high nitrogen loads (Huber and Kreutzer 2002; Rothe et al. 2002; Huber et al. 2002). Furthermore, these stands appear uniform, with a low value for nature conservation.

Currently, one goal of the official forest management administration in Bavaria is to transform pure coniferous stands into mixed forests. From 1987 to 2002, the proportion of areas with broadleaf trees has increased from 22 to 30% (Rothe and Borchert 2003). In the next years, more than 100,000 ha of conifer-rich forests will be converted into mixed forests with efforts focused in the southern part of Bavaria.

Two methods are widely used in this region to promote regeneration in forests: the farmers in private forests make small clear-cuts of the size of 0.5 to 1 ha, and the Bavarian State Forest Administration are regenerating the stands with selective cutting of the trees (group shelterwood system).

We have studied at the Höglwald site the early impacts of regeneration on soil fertility, seepage water quality, emission of nitrogen trace gases, and the diversity of ground vegetation and fauna. We compared the effects of a shelterwood system (regenerated with beech), and a small clear-cut (regeneration with beech, or spruce). The small clear-cut may also be used as a model for open areas in the forest due to storm events, which have occurred frequently in recent years in this region. Pre-treatment samples were collected in 1999, and felling was done the following spring.

In this paper we studied the influence of the above mentioned regeneration methods on ground beetles (Coleoptera: Carabidae). In recent years the investigations about the change of carabid assemblages according to forest management practices has increased (for example Assmann 1999; Werner and Raffa 2000; Heliölä et al. 2001; Koivula 2002; Magura et al. 2000, 2003; Poole et al. 2003). However, there is a lack of knowledge about (1) the fast response in the critical phase, directly after the cutting, and (2) the effect of different methods of forest regeneration including small clear-cuts and selective cutting.

Our hypotheses are: (I) small scale clear-cut affects ground beetle assemblages in the same way as Niemelä et al. (1993) reported for larger clear-cuts:

- (a) species richness increases,
- (b) species typical for open habitats increase,
- (c) forest species decrease, but are still present on the regeneration sites,
- (d) some forest specialists fail to colonise these stands; and (II) selective cutting nearly preserves the original assemblages of carabids.

To test these hypotheses, our main objectives were to determine the change in diversity, number of individuals, species composition, and to further explain patterns of occurrence of ground beetle assemblages. To better understand the impact of a possible rapid response of forest cutting to carabid assemblages, we measured various abiotic and biotic parameters like photoactive radiation, precipitation, and diversity and coverage of the ground vegetation. Also, the number of individuals of other faunistic groups (snails, spiders, springtails, other beetles) were included in the investigation.

Materials and methods

Site description

The Höglwald site is a long-term ecological monitoring and experimentation site. The research at the site started in 1983, with the main focus on biogeochemistry and ecosystem research. For more details about the stand and site characteristics see Kreutzer and Bittersohl (1986), Kreutzer et al. (1991), and Kreutzer and Weiss (1998). The forest district of the Höglwald (370 ha) is situated in the hilly landscape of southern Bavaria, Germany about 70 km north of the Alps and 50 km west of Munich (centre) at 11°11'E and 48°30'N. The forest is situated on a flat hill-top at an altitude of 540 m above sea level, surrounded by intensively managed farmland (cattle breeding, dairy, and maize). The proportion of agricultural land to forest land (predominantly small conifer forests) is approximately 2:1 (Kreutzer and Weis 1998). The climate is suboceanic. The region belongs to the temperate broad-leaf zone, originally dominated by beech. For the period 1984 to 2001, mean annual precipitation at the Höglwald forest was 933 mm, mean annual temperature 7.7 °C, mean difference between the warmest and the coldest month 17.5 °C, and the mean number of days exceeding 10 °C mean temperature 155. During the observation period from 1999 to 2001, the climatic data differed from the long-term means. The mean temperature in this period was 8.2 °C and the mean bulk precipitation amounted to 1161 mm on average. The soil is a parabrown earth (Central European System) (USGS: Typic Hapludalf; FAO: Dystric Cambisol), strongly acidified in the top soil and weakly aquic in the argillic horizon. The mineral soil is covered by an organic layer 6–8 cm thick. The humus form is moder. In the mineral soil, no coarse material is present. In the organic layer, the base saturation of the cation exchange capacity is relatively high (40–80%), whereas the pH values are extremely low with a minimum in the Oh horizon with 2.75 (KCl). The base saturation in the A horizon is low (5–10%) and the aluminium saturation is high (80–90%), with pH values around 4.0–4.5. In the B horizon, the base saturation increases with depth as well as pH values. The C/N ratio varies in forest floor between 23 and 27. The site is nitrogen oversaturated, with a throughfall input of 30 kg N ha⁻¹ y⁻¹ (Rothe et al. 2002), NO₃⁻ leaching via seepage of

1992

approximately $30 \text{ kg N ha}^{-1} \text{ y}^{-1}$ (Rothe et al. 2002), and relatively high emissions of N-trace gases of approximately 8 kg N in the form of N_2O and N (Butterbach-Bahl et al. 2002). The investigated stands are mature Norway spruce plantations, (*Picea abies* (L.) Karst), second generation after beech (*Fagus sylvatica* L.), cultivated in 1910/11 with 3- or 4-year-old plants. The natural vegetation type is classified as submontane *Asperulo-Fagetum luzu-letosum*, an acidophytic community transient to *Luzulo-Fagetum oxalidetosum*. The spruce stand is growing vigorously, is full-stocked, and has a closed canopy. The last thinning was performed in 1975. The ground vegetation is dominated by mosses.

Experimental treatments

In an area with very uniform stand and site conditions the following treatments were carried out:

1. C: control plot (in other investigations named A1);
2. S: selective cutting (0.9 ha), regeneration with planted beech trees;
3. CC: small scale clear-cut (1.0 ha) divided into the following two parts;
4. CCB: clear-cut, regeneration with planted beech trees (0.5 ha);
5. CCS: clear-cut, regeneration with natural or planted spruce (0.5 ha).

The experimental plots are separated by fences and small roads. The felled plot is situated in the centre of the tree plots, 250 m NE is the control plot, and 150 m SE the clear-cut plot, which was separated in a part planted with spruce sapling, and in a part planted with beech saplings.

In 1999 the experimental plots were installed. The felling was performed with a harvester in February 2000. Stems including bark were removed, slash remained on the plots. Selective cutting was performed removing 20% of the trees in an area of approximately 0.9 ha, following planting of beech saplings. The clear-cut was divided in a part regenerated with beech and a part regenerated with spruce. Five-year old saplings (beech or spruce) were planted in March 2000. On a small part of the CCS 5–10-year-old spruce trees are growing, originating from seedlings of the mature stand (natural regeneration). On the clear-cut investigations were concentrated in the centre of each subplot, to diminish the influence from surrounding habitat.

Experimental methods

At each plot 10 pitfall traps, 6 emergence traps, and 6 window traps were installed. The traps were established in each stand by placing the traps randomly close to the centre of each plot (ca. 5–10 m apart from each other), close to other investigations made on the plots (for example elemental concentrations in seepage water, emission of trace gases, meteoro-

logical measurements). The trapping stations were set at > 150 m from the edge of the forest to avoid edge effects (Magura et al. 2002). At the small scale clear-cut, the distance between traps on CCB and traps on CCS, and the distance to the nearest stand edge was ca. 25 m (see also Koivula et al. 2002). The trapping period covered most of the growing season (May–October). The animals were collected three times a year (spring, summer, and autumn). The traps were emptied 2 weeks after positioning. All captured animals were transferred in 70% isopropanol and assigned to taxonomic groups. Pitfall traps were plastic jars (diameter 75 mm, depth 100 mm) partly filled with 1% ethyleneglycol. A transparent plastic roof (18 cm × 18 cm) was placed some centimetres above the trap to prevent flooding from rainwater. Emergence traps (Ecotech) were cone-shaped tents without bottom. The brink of the tent is worn in the humus layer, a pitfall trap is at the bottom, and on top of the tent a box is fixed containing coppersulphate (1%). Window traps (Eco Tech) were fixed at 2.5 m height with an aluminium tripod. The trap consists of two transparent plastic windows (80 cm × 50 cm) fixed vertical to each other. On top and bottom a funnel with a box containing coppersulphate (1%) is fixed to collect the flying insects. The coverage of different species of ground vegetation close to the pitfall traps (2 m) was estimated for all years. Besides ground beetles the number of individuals of other groups of animals were also counted. We included in this investigation: springtails (separated in the groups Symphypleona and Entomobryomorpha), other groups of beetles (Staphylinidae, Curculionidae, and Elateridae), and different groups of spiders (Araneidae in total, and separated into Lycosidae, Linyphiidae, and Amaurobiidae) and used as environmental variables in the multivariate analyses. Photoactive radiation (PAR) was measured at 1 m height with a Licqor Par sensor. The measurements were used in detrended correspondance analysis (DCA; Hill and Gauch 1980), using the PC-ORD4 software package for Windows (McCune et al. 2002). We first studied whether the two regeneration methods (clear-cutting, or selective cutting) affect the total catches (pitfall + emergence + window traps) of carabids. We excluded from the analysis carabid species with two or less individuals per plot and year. After these modifications, we included in the analysis 16 environmental variables and 24 carabid species. Second, we studied the effects of forest regeneration on single pitfall traps. Seventeen species, 15 environmental factors, and 101 pitfall samples (yearly values) were included in the analysis. Nine pitfall samples were excluded from the study, which exhibited less than two individuals per species observed. Whether the carabid beetles assemblages on the plots differed in size was studied performing ANOVAs (SPSS 11.5.1, SPSS Inc.) for each year of investigation. Bonferroni *post hoc* tests were performed for uniformity in variance, Tamhane T2 when the variance was not equal. The distinctions about size and habitat preference were made by referring to literature (Lindroth 1945; Freude et al. 1976; Thiele 1977; Makeschin and Habereeder 1991; Marggi 1992).

Results

In the 3 years of investigation 33 species and 3879 individuals of carabid beetles were sampled on the investigation plots. Ninety percent of the catches were made on the ground (80 in pitfall traps, 10 in emergence traps), and 10% were caught with window traps (Figure 1). Yearly 9–11 species were found on each mature spruce plot (control plot, or on the other plots prior to cutting). On the selective-cutting plot the number of species was slightly elevated in the year of cutting, and decreased in the first year after the cutting. On the clear-cut plot the highest catches were made in the year of cutting (2000). Most individuals were caught in the window traps on the clear-cuts, whereas the number of individuals on the ground was nearly equal compared to the other plots. The number of species caught per year was increased from 11 to 23 after the clear-cut. However, in 2001, individuals decreased on the clear-cut plots. The number of species also decreased, but was still higher than before the experiment. In the year of the clear-cut, more species were sampled in the pitfall-traps of the clear-cut (CCB and CCS) than on selective cutting (S), or on the control plot (C). Smaller and winged species colonised the clear-cut. Therefore, the average size of carabids on the clear-cut is significantly smaller than on the control plot (Figure 2), whereas it was larger in the pre-treatment period. On the clear-cut plots a higher percentage of typical open habitat species could be found after the felling (Figure 3). On the clear-cut plot regenerated with spruce

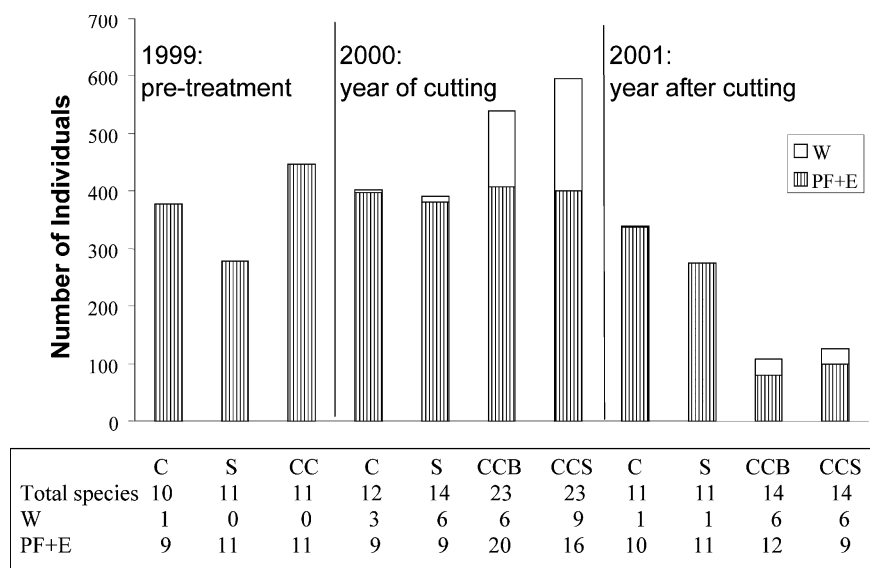


Figure 1. Number of carabid individuals (graph) and species (table) before and after cutting in window (W), pitfall (PF), and emergence (E) traps in the years 1999 (pre-treatment), 2000 (year of cutting), and 2001 (year after cutting).

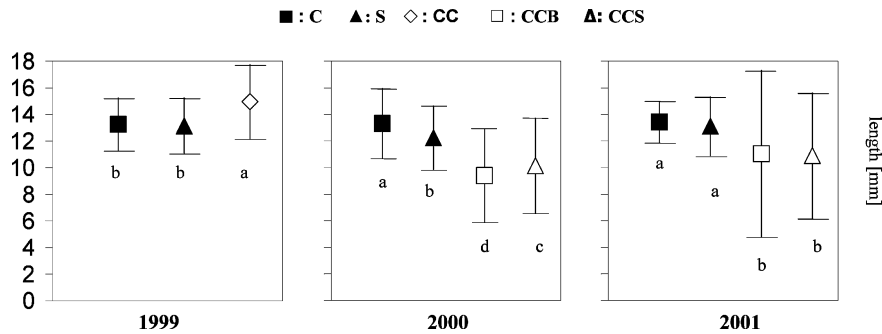


Figure 2. Average length \pm S.D. of carabids in the years 1999 (pre-treatment), 2000 (year of cutting), and 2001 (year after cutting). Different letters indicate a significant ($p < 0.001$) difference. C: control; S: selective cutting; CC: clear-cut in pre-treatment period, later divided into CCB: clear-cut beech, and CCS: clear-cut spruce.

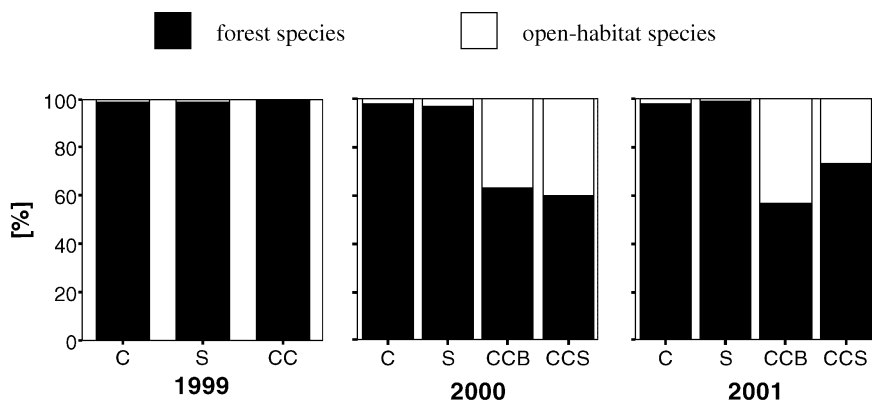


Figure 3. Proportion of forest species, and open-habitat species in the years 1999 (pre-treatment), 2000 (year of cutting), and 2001 (year after cutting). C: control; S: selective cutting; CC: clear-cut in pre-treatment period, later divided into CCB: clear-cut beech, and CCS: clear-cut spruce.

37% of the total catches were open habitat species, normally not present with high numbers of individuals in the mature forest ($< 1\%$ before felling).

In 3 years 19 species occurred on the control plot (Table 1); however, some of these only with 1 or 2 individuals per year. The most numerous species were *Pterostichus oblongopunctatus*, *Pterostichus burmeisteri*, and *Abax parallelepipedus*. These three species represented 85–91% of the total yearly catches. *Pterostichus oblongopunctatus* and *Pterostichus burmeisterii* were still the dominating species after the clear-cut (Table 1); however, the number of individuals was drastically lower. Only one individual of *Abax parallelepipedus*, subdominant before the clear-cut, was found on the two clear-cut plots in 2001. *Trechus quadristatus* was the second most common species in the year following the clear-cut on CCB (clear-cut beech), *Bradycellus harpalinus* the third

Table 1. Total catches of carabid beetles in 1999 (pre-treatment), 2000 (year of cutting), and 2001 (year after cutting). C: control; S: selective cutting; CC: clear-cut in the pre-treatment period, later divided into CCB: clear-cut beech, and CCS: clear-cut spruce.

Species	Hab	Size (mm)	Abbr.	1999 : pre-treatment		2000 : year of cutting				2001 : year after cutting				
						C		S		C		S		
				C	S	CC	C	CCB	CCS	C	S	CCB	CCS	
<i>Abax parallelepipedus</i> (Piller et Mittelpacher, 1783)	F	18.5	Abaxpara	49	29	78	32	26	2	6	35	24	1	0
<i>Abax parallelus</i> (Dufschmied, 1812)	F	15.0		0	0	1	0	0	0	0	0	0	0	0
<i>Agonum muelleri</i> (Herbst, 1785)	O	8.0	Agonmuel	0	0	0	1	2	7	33	0	0	0	0
<i>Agonum sexpunctatum</i> (L., 1758)	O	8.3	Agonsexp	0	0	0	0	0	7	3	0	0	0	2
<i>Amara curta</i> (Dejean, 1828)	O	6.8	Amarcurt	0	0	0	2	0	5	8	0	0	13	8
<i>Amara similata</i> (Gyllenhal, 1810)	O	8.8	Amarsimi	0	0	0	0	0	1	6	0	2	6	2
<i>Anisodactylus binotatus</i> (Fabricius, 1787)	O	11.0	Anisbino	0	0	0	0	1	2	0	1	0	11	10
<i>Bembidion humerale</i> (Sturm, 1825)	O	2.8	Bembhume	0	0	0	0	0	2	2	0	0	8	5
<i>Bembidion quadrimaculatum</i> (L., 1761)	O	3.2	Bembquad	0	0	0	0	0	19	6	0	0	0	0
<i>Bradycellus harpalinus</i> (Serville, 1821)	O	4.1	Bradharp	0	0	0	0	0	10	58	0	0	0	4
<i>Carabus cancellatus</i> (Illiger, 1798)	O	24.5	Carabcanc	0	0	0	0	0	2	2	0	0	2	1
<i>Carabus coriaceus</i> (L., 1758)	F	35.0	Carabcori	2	4	7	5	4	4	7	4	5	6	3
<i>Carabus granulatus</i> (L., 1758)	F	24.5		0	0	1	0	0	1	0	0	0	0	0
<i>Carabus hortensis</i> (L., 1758)	F	35.0	Carabhorr	18	10	51	23	10	4	18	8	3	3	1
<i>Carabus nemoralis</i> (Müller, 1764)	F	24.5	Carabnemo	8	11	2	14	9	1	2	17	10	0	4

Table 1. Continued.

Species	Hab	Size (mm)	Abbr.	1999 : pre-treatment						2000 : year of cutting						2001 : year after cutting									
				C		S		CC		C		S		CCB		CCS		C		S		CCB		CCS	
				C	S	C	S	CC	CC	C	S	C	S	CCB	CCS	CCS	C	S	C	S	CCB	CCS	CCS	CCS	
<i>Diachromis germanus</i> (L., 1758)	O	9.0				0	0	0	0	0	0	1	0	0	6	0	0	0	0	0	0	0	0		
<i>Dromius agilis</i> (Fabricius, 1787)	F	6.1				1	0	0	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Harpalus latus</i> (L., 1758)	O	9.5				0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0		
<i>Harpalus griseus</i> (Panzer, 1797)	O	10.0				0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0		
<i>Harpalus rufipes</i> (De Geer, 1774)	O	13.5				0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0		
<i>Loricera pilicornis</i> (Fabricius, 1757)	O	7.0				1	1	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0		
<i>Microlestes minutulus</i> (Goetze, 1777)	O	3.1				0	0	0	0	0	0	2	2	0	2	0	1	0	0	1	0	0	0		
<i>Nebria brevicollis</i> (Fabricius, 1792)	F	11.5				0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0		
<i>Notiophilus biguttatus</i> (Fabricius, 1797)	F	4.5				3	3	0	5	3	2	4	2	4	2	1	12	14	1	1	12	14	14		
<i>Poecilus cupreus</i> (L., 1758)	O	11.0				0	0	0	0	0	0	20	13	0	0	0	4	2	0	0	4	2	2		
<i>Pterostichus burmeisteri</i> (Heer, 1841)	F	13.3				96	51	136	109	69	82	113	121	121	121	90	15	28	0	0	15	28	28		
<i>Pterostichus melanarius</i> (Illiger, 1798)	O	15.0				0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Pterostichus oblongopunctatus</i> (Fabricius, 1787)	F	10.5				197	163	168	208	254	245	207	141	136	23	42	0	0	0	0	0	0	0		
<i>Pterostichus vernalis</i> (Panzer, 1796)	O	6.7				0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Stenolophus teutonius</i> (Schränk, 1781)	O	6.3				0	0	0	0	0	1	6	56	0	0	0	0	0	0	0	0	0	0		
<i>Trechus quadristriatus</i> (Schränk, 1781)	O	4.0				2	0	0	3	7	113	39	5	0	2	0	0	0	0	0	2	0	0		
<i>Trichotichus laevicollis</i> (Duftschmied, 1812)	F	7.5				0	3	1	0	3	1	1	4	2	0	0	0	0	0	0	2	0	0		

Hab: habitat preference type. F: forest species; O: open-habitat species. Abbr.: abbreviations for species names used in the DCA. The distinctions about size and habitat preferences were made by referring to literature (Lindroth 1945; Thiele 1977; Freude et al. 1976; Makeshin and Habereeder 1991; Marggi 1992).

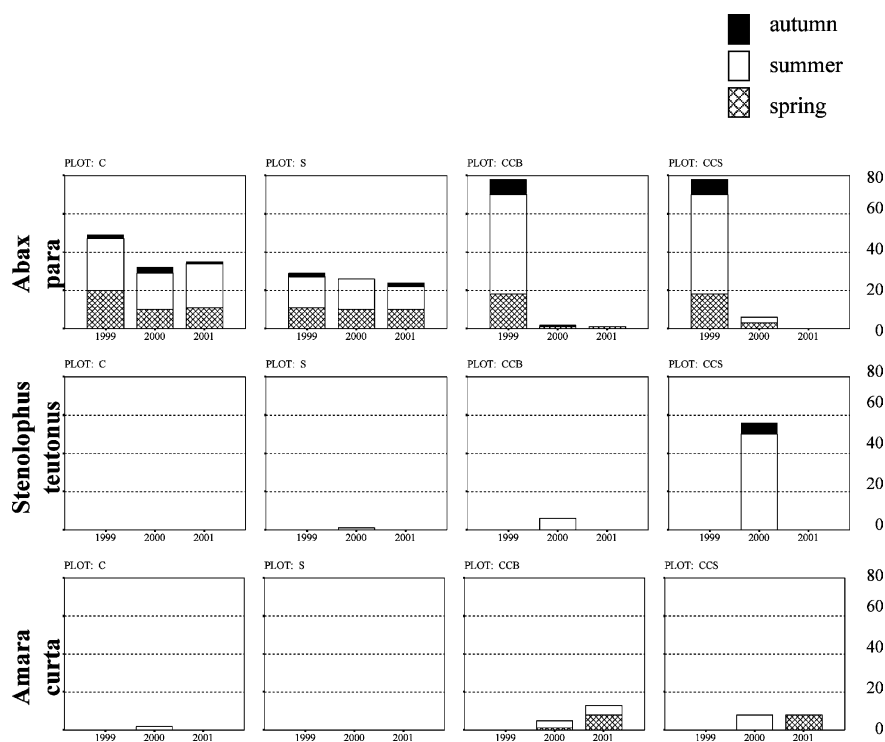


Figure 4. Number of individuals of three different carabid species in the sampling periods (spring, summer, autumn) in the years 1999 (pre-treatment), 2000 (year of cutting), and 2001 (year after cutting). C: control; S: selective cutting; CCB: clear-cut beech; CCS: clear-cut spruce; *Abax para.*: *Abax parallelepipedus*. Note: in the pre-treatment period CCB and CCS was a single plot.

most common species on CCS (clear-cut spruce). However, both were almost completely captured in the window traps, and were nearly absent in the following year. In 2001 *Amara curta* on CCB and *Notiophilus biguttatus* on CCS were the third most common species on both clear-cutting plots. Individuals of the three dominating species represented 82% (2000) and 48% (2001) on plot CCB, and 64% (2000) and 67% (2001), respectively on plot CCS of the total individuals. Figure 4 presents the catches of three different species, typical for changes in carabid assemblages after the felling. The catches of the forest specialist *Abax parallelepipedus*, subdominant on all plots before felling, decreased immediately in the first sampling period after the felling. *Stenolophus teutonius* is typical for some open habitat species, and appeared only on the logged plots in the year 2000. In the next year, the species decreased and finally disappeared on the clear-cut plots. *Amara curta* is an example of a species which appeared in the first sampling after the felling on the clear-cut plots, and could be found also in the next year on both clear-cut plots.

In the DCA of the total catches (Figure 5), the mature spruce plots (S, CCB, CCS in the pre-treatment period, and plot C in the prevailing years) together

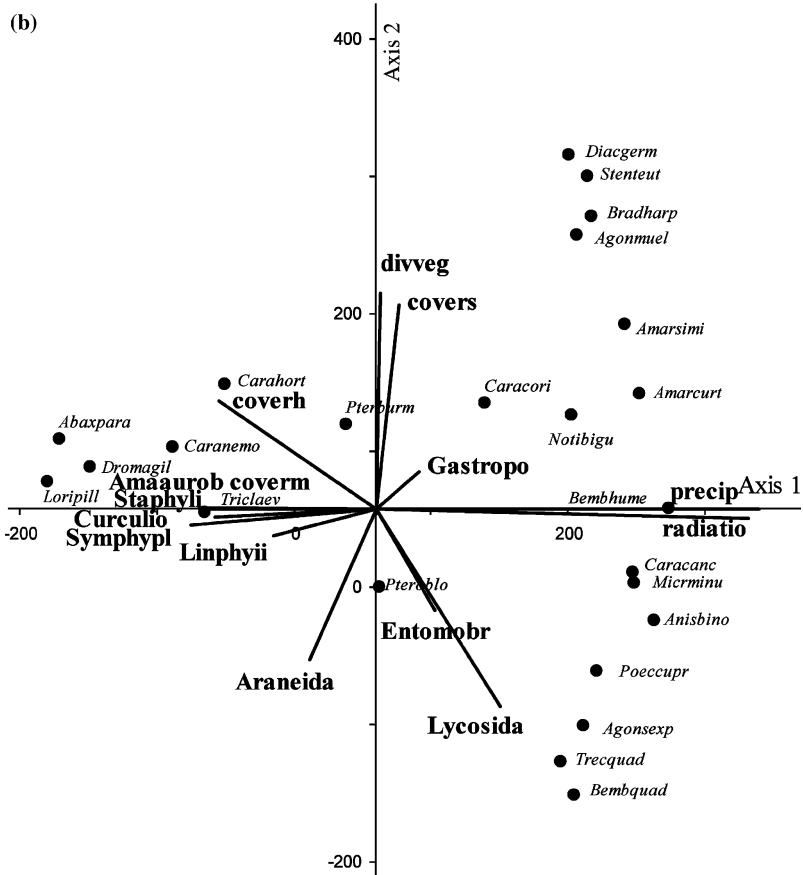
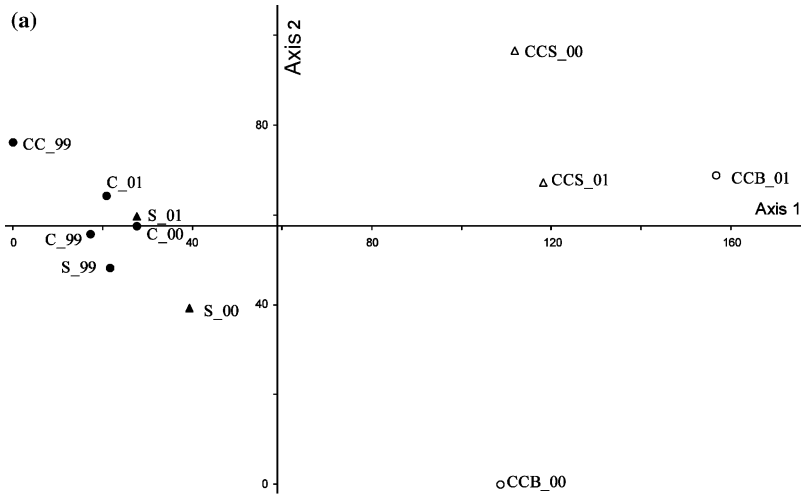
with the selective-cut plot (S) are clearly separated from the clear-cut plots (after felling). The total variance of the data was 0.683. The eigenvalue of the two axes were 0.279 (axis 1), and 0.104 (axis 2). The abbreviations of the species can be found in Table 1. Most forest species, or forest specialists, were clustered to the left of the ordination: *Abax parallelepipedus*, *Dromius agilis*, *Carabus hortensis*, *Carabus nemoralis*, and *Trichotichnus laevicollis*. *Pterostichus oblongopunctatus*, and *Pterostichus burmeisteri* were close to the center of axis 1. Coverage of mosses, coverage of herbs, different net building spiders (Amaurobiidae and Lycosidae), other groups of beetles (Curculionidae and Staphylinidae), and Symphyleona (Collembola) were on the optimum left to the origin of the ordination. The carabid species clustered on the left side of our DCA are regularly larger than the species clustered on the right side and have low or no flight capabilities. Nearly all open habitat species (fallow land, grassland, cultivated land, and wetland species), or some generalists, often with flight capabilities, were clustered to the right side. Factors reflecting clear-cut conditions (higher radiation, and precipitation on axis 1) together with higher coverage of shrubs, and diversity of ground flora (positive with axis 2) were at their optimum top and right of the origin. There we find species appearing in the first year of clear-cutting, which favour plant habitats or are herbivores: *Diachromus germanus*, *Stenolophus teutonius*, *Bradycellus harpalinus*, and *Agonum muelleri*. On the right side of axis 1 and closer to the centre of axis 2, we find species appearing also in the first year after the clear-cut: *Amara similata*, *Amara curta*, *Bembidion humerale*, and *Anisodactylus binotatus*. The first three species are also common in riparian and moor ecosystems. *Bembidion humerale* may profit from disturbances like locally occurring water-filled ruts, caused by the harvester on the loamy soil. Also, snails tend in this direction of the DCA. At the bottom species are clustered favouring lower covering of ground vegetation, and shrubs: *Agonum sexpunctatum*, *Bembidion quadrimaculatum*, *Trechus quadristriatus*, and *Poecilus cupreus*. These species seem to have same preferences like the Lycosidae (wolf spiders), a free hunting (without nets) spider family. In the same direction the group of Entomobryomorpha (Collembola) have their optimum.

The multivariate analyses from all pitfall traps showed nearly the same result as the analyses of the total catches (Figure 6). However, the figure clearly shows that nearly all pitfall traps from the selective cutting, and the control plots are separated from the traps of the clear-cut plots. The majority of traps on selective cutting and control plots are clustered to the left or in the centre. Traps from the clear-cut are clustered right from the origin. However, few traps of the selective cutting plots are close to traps of the first year of clear-cutting.

Discussion

Species richness of carabids increased in the year after a small scale clear-cut (2000) in the Höglwald forest. An increased diversity of carabid assemblages

2000



after clear-cut was also found in boreal forests of Canada and Finland (Niemelä et al. 1993; Heliölä et al. 2001; Koivula et al. 2002), in Norway spruce stands in Hungary (Magura et al. 2002), and numerous other studies with a broad range of forest types all over the world (see Niemelä et al. 1993). Our results are in agreement with Niemelä et al. (1993), who postulated a 'general response of ground beetles to clear-cutting'. Initially, species typical for open habitats increase and forest species decrease (see also Koivula 2002). It is a common trend that large poorly dispersing specialists decrease with increased disturbance, while small generalist species with good dispersal abilities increase (Rainio and Niemelä 2003). Many open habitat species occurred in our study within a few months of treatment on the small clear-cut, and had good flight capabilities according to Marggi (1992) or Thiele (1977). A certain proportion were therefore caught in the window traps; however, most of them only in the year after felling. Also, Magura et al. (2003) found the highest number of individuals capable of flying in recently established plantations. A rapid colonisation of open habitat species was also recognised in the study of Koivula (2002) and Heliölä et al. (2001). The edge of the forest (Molnar et al. 2001), open areas in the forest, or the surrounding fields may serve as the source of the open habitat species. Occasionally, we found at the Höglwald site individuals of open habitat species also in the mature stands, even in parts 1 km or more from the forest edge. We assume that a certain proportion of open habitat species also occur already in the forest in small 'natural' openings. Like Niemelä et al. (1993), we found an increase in open grassy habitat species after the small clear-cut. Additionally, open habitat species more typical of moor and riparian ecosystem (for example *Bembidion humerale*) occurred, most probably because of water-filled ruts after soil compression caused by the harvester. At the scale of meters the small clear-cut, which seems to be homogenous, is obviously more patchy than the mature stand at the Höglwald site, explaining the small scale abundance variation of carabid beetles. According to the results of the DCA, the species separate into different groups: closed canopy species, generalists, and open phase specialists. Staphylinidae, Curculionidae, some families of spiders (Amaurobiidae, and Linyphiidae), and the Symphypleona (Collembola) responded in the same way as the closed canopy species of the



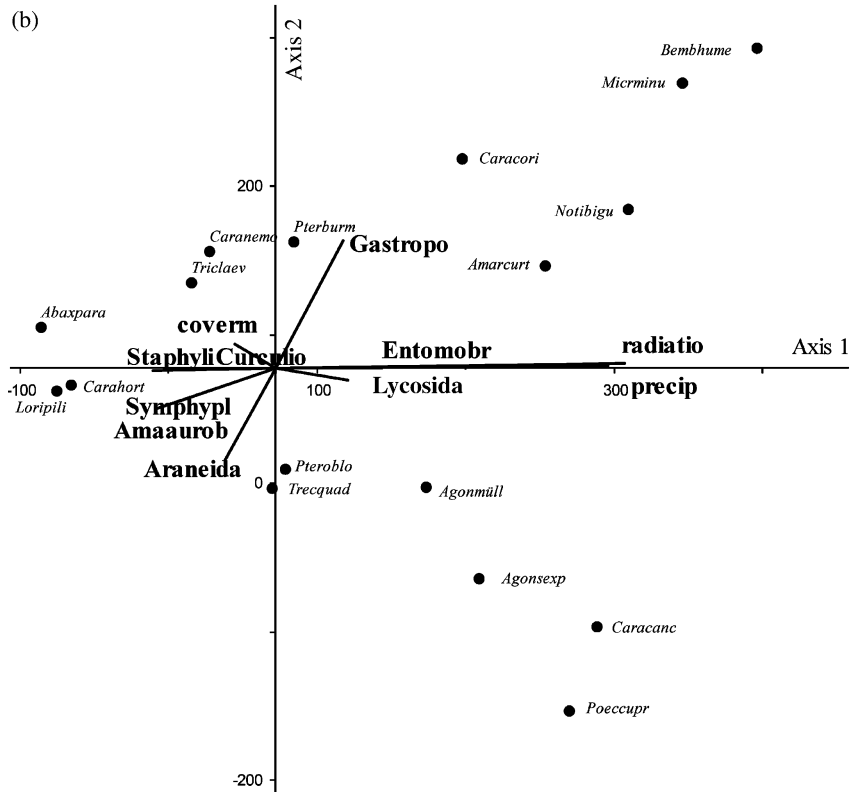
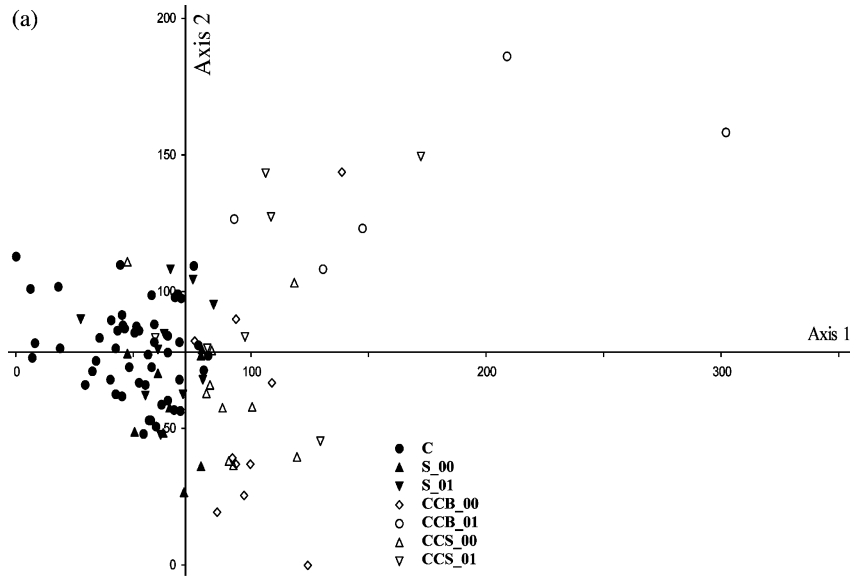
Figure 5. (a) DCA ordination for the stands used to study total carabid assemblages (pitfall, emergence, and window traps) in the years 1999 (pre-treatment), 2000 (year of cutting), and 2001 (year after cutting). C: control; S: selective cutting; CCB: clear-cut beech; CCS: clear-cut spruce; _99: year 1999; _00: year 2000; _01: year 2001. (b) DCA ordination of 24 species caught during 1999–2001. The eight-letter abbreviations indicate the species, e.g., Carahort: *Carabus hortensis*. Abbreviations of the carabid species are listed in Table 1. Label explanations: Gastrop: number of individuals of Gastropoda; Lycosida: Lycosidae; Entomobr: Entomobryomorpha; Araneida: Araneidae; Linphyii: Linyphiidae; Symphyp: Symphypleona; Curculio: Curculionida; Staphyli: Staphylinidae; Amaurob: Amaurobiidae; divveg: number of species of ground vegetation; precip: precipitation; radiatio: photosynthetic active radiation; coverh: coverage of herbs; coverm: coverage of mosses. Note that the scales of the axes in (a) and (b) are different.

carabids. The small clear-cuts are characterised by higher radiation, soil temperature, and precipitation. The DCA gave indications that some open habitat carabid species responded to the diversity of ground vegetation and coverage of shrubs. *Diachromus germanus*, *Stenolophus teutanus*, *Bradycellus harpalinus*, and *Agonum mülleri* aggregated in this direction in the DCA. All of them are herbivores, or prefer higher ground vegetation (Maggi 1992). However, why they were absent in the year after cutting remained unclear. There are indications in the DCA that *Agonum sexpunctatum*, *Trechus quadristriatus*, and *Bembidion quadrimaculatum* prefer the same patterns as the Lycosidae, a family of free hunting spiders. The abundance of some carabids correlated positively with the gastropoda, indicating more food resources for some species (*Notiophilus biguttatus*), or a preference for moist patches (for example *Bembidion humerale*, *Amara curta*, and *Amara similata*).

However, like larger clear-cuts in other investigations (Niemelä et al. 1993; Koivula et al. 2002; Magura et al. 2002), the small scale clear-cuts became a threat for forest generalists or forest specialists. Two of the three most abundant forest species decreased after the clear-cut at the Höglwald site, but were still present with a relatively high number of individuals. *Pterostichus oblongopunctatus* and *Pterostichus burmeisteri* maintained relatively large populations after the clear-cut. They seem to be more flexible than other forest species and may recover with higher numbers of individuals after the stand becomes denser. In a Finnish study *P. oblongopunctatus* could even benefit from clear-cut, edge effects (Heliölä et al. 2001), and gap felling (Koivula and Niemelä 2003). In the second year, after the harvesting *Abax parallelepipedus* was present with just one individual on the two clear-cut plots. In the pre-treatment period, we found even higher number of individuals on the clear-cut plots, which were situated closer to an old beech stand, than on the other plots. This is in good agreement with the general assumption that *A. parallelepipedus* in this region is a typical forest species (Freude et al. 1976; Thiele 1977; Maggi 1992). Also, Engel (1999) found in southern Germany the highest numbers of individuals of *A. parallelepipedus* in an old beech forest, and the lowest numbers in a regenerating spruce forest. Conversely, in investigations made in Hungary and Ireland, *Abax parallelepipedus* was present in all habitats, including grasslands (Molnar et al. 2001; Poole et al. 2003). *Carabus nemoralis* was even totally absent in the year on the



Figure 6. (a) DCA ordination for single pitfall traps in the years 1999 (pre-treatment), 2000 (year of cutting), and 2001 (year after cutting). C: control; S: selective cutting; CCB: clear-cut beech; CCS: clear-cut spruce; _99: year 1999; _00: year 2000; _01: year 2001. (b) DCA ordination of 18 species caught during 1999–2001. The eight-letter abbreviations indicate the species, e.g. Carahort: *Carabus hortensis*. Abbreviations of the carabid species are listed in Table 1. Label explanations: Gastrop: number of individuals of gastropoda; Lycosida: Lycosidae; Entomobr: Entomobryomorpha; Araneida: Araneidae; Symphyp: Symphypleona; Curculio: Curculionida; Staphyli: Staphylinidae; Amaurob: Amaurobiidae; precip: amount of precipitation; radiatio: yearly photosynthetic active radiation; coverm: coverage of mosses. Note that the scales of the axes in (a) and (b) are different.



clear-cut plot regenerated with beech; however, the species was present with low numbers of individuals on dense parts of natural spruce regenerating patterns. In a Hungarian study, the species was found in all habitats (Molnar et al. 2001). In contrast to *A. parallelepipedus*, *Notiophilus biguttatus* seems to benefit from the clear-cut, especially in the first year after cutting. This was in agreement with the results of Koivula (2002) in boreal forests.

In our study the open habitat species increased markedly in abundance after the cutting. Together with the persistence of several mature forest generalists, carabid diversity was therefore increased on the clear-cut compared to selective cutting, or the control plot. However, other investigated groups of arthropods, like Staphylinidae, Curculionidae, and spiders were less frequent or did not differ in the clear-cut compared to the mature forest (data not presented). Also the number of carabid species decreased already in the year after the cutting; however, the number of species was still slightly higher than before the cutting. Magura et al. (2003) found that clear-cutting may result later in lower carabid diversity. They found fewer species in 5, 15, 30 and 50 yr. old Norway spruce plantations.

In the mature stand, we found a relatively low species richness, with a few species dominating. The species composition was in good agreement with a study made in 1986/87C (Makeschin and Haberer 1991) at the Höglwald site, focusing on acid irrigation and forest liming. Like Makeschin and Haberer (1991), we found at the Höglwald site a few abundant species and many scarce species, but no intermediately common ones. This was also reported from Niemelä et al. (1993) for a boreal forest.

Selective cutting at the Höglwald site conserved the species assemblages of the mature stand. The DCA analyses showed that most pitfall trap assemblages on the selective-cut plot were similar to mature forest, few were comparable to the assemblages of the clear-cuts. Also, Koivula (2002) found that stands with small openings best maintained the original assemblage structure. However, it is unclear what happens after additional felling on the selective cutting plots at our site. Further investigations are needed to clarify the question, if the planted beech regeneration, becoming denser over time, can be a substitute for the removed mature spruce canopy, to preserve the forest species. If this is not the case, enough area of mature trees should be left as a possible retreat for forest species, until the conditions are sufficient so that the beetles may inhabit the logged and regenerated area again.

The number of species is one important variable impacted by forest management decisions directed by forest policy. However, the concept of maximum species richness as the most important resource management goal for forests needs to be more carefully considered (Lindenmayer 1999). For example, in our case, maximum species diversity occurred in the year after clear-cutting, because of the invasion of species with open field or fallow field character (see also Niemelä et al. 1993), and the persistence of most forest species. Because of the fast response, these species are most probably also present in (non-investigated) other open parts of the forest, or in the open fields (agricultural land)

close to the stand. On the other hand, forest species disappeared on the clear-cut, or the number of individuals was drastically reduced. If clear-cuts become the dominant landscape element, they may threaten the existence of mature forest specialists and in the long run of forest generalists (see Niemelä et al. 1993). However, small openings after clear-cut, or storm events in restricted areas of forests can serve as important retreat for some open habitat species. With selective cutting, species richness is not improved immediately; however, there chance is a greater to preserve the remaining carabid assemblages of the mature spruce stand, and to protect forest generalists and forest specialists. The results of Koivula et al. (2002) indicate that forest species thrive in a heterogeneous mosaic of differently aged stands. Therefore, the initiation of regeneration should be spread over a longer space of time. Also, varying the cutting regimes has potential benefits including reducing the risk of homogenising landscape patterns (Lindenmayer 1999). Different structures side by side (mature forest stand, selective cutting, small scale clear-cut, different mixtures of site-specific tree species) could also improve diversity at the Höglwald site. However, in addition other current problems of nitrogen saturated stands (N_2O emissions, NO_3^- leaching) must be considered when choosing a management strategy.

Acknowledgements

The work was funded by the Bundesministerium für Bildung, Forschung und Technologie (BMBF), under contract number 0339733A. The authors would like to thank Florian Busl for identification of carabid species. Angela Alkofer and Manfred Gibis did great work in the field as well as in sorting the different faunal groups. Kerstin Engel, Rüdiger Detsch, and Uli Simon are thanked for their advice before the experiment. We thank Jared David May for proof-reading the manuscript. We are grateful that the reviewers thoroughly checked the manuscript and helped to improve the manuscript with their valuable comments.

References

- Assmann T. 1999. The ground beetle fauna of ancient and recent woodlands in the lowlands of north-west Germany (Coleoptera, Carabidae). *Biodiversity and Conservation* 8: 1499–1517.
- Butterbach-Bahl K., Gasche R., Huber C., Kreutzer K. and Papen H. 1998. Impact of N-input by wet deposition on N-trace gas fluxes and CH_4 -oxidation in spruce forest ecosystems of the temperate zone in Europe. *Atmospherical Environment* 32: 559–564.
- Butterbach-Bahl K., Gasche R., Willibald G. and Papen H. 2002. Exchange of N-gases at the Höglwald Forest – A summary. *Plant Soil* 240: 117–123.
- Engel K. 1999. Analyse und Bewertung von Umbaumaßnahmen in Fichtenreinbeständen anhand ökologischer Gilden der Wirbellosen-Fauna. Wissenschaft & Technik Verlag, Berlin, Germany.
- Freude H., Harde K.W. and Lohse G.A. 1976. Die Käfer Mitteleuropas. Goecke und Evers, Krefeld, Germany.

- Heliölä J., Koivula M. and Niemelä J. 2001. Distribution of carabid beetles (Coleoptera, Carabidae) across a Boreal forest-clearcut ecotone. *Conservation Biology* 15: 370–377.
- Hill M.O. and Gauch H.G. 1980. Detrended correspondence analysis: an improved ordination technique. *Vegetatio* 42: 47–58.
- Huber C. and Kreutzer K. 2002. Three years of continuous measurements of atmospheric ammonia concentrations over a forest stand at the Höglwald site in southern Bavaria. *Plant Soil* 240: 13–22.
- Huber C., Oberhauser A. and Kreutzer K. 2002. Deposition of ammonia to the forest floor canopies under spruce and beech at the Höglwald site. *Plant Soil* 240: 3–11.
- Koivula M. 2002. Alternative harvesting methods and boreal carabid beetles (Coleoptera, Carabidae). *Forest Ecology and Management* 167: 103–121.
- Koivula M., Kukkonen J. and Niemelä J. 2002. Boreal carabid-beetle (Coleoptera, Carabidae) assemblages along the clear-cut originated succession gradient. *Biodiversity and Conservation* 11: 1269–1288.
- 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.
- Kreutzer K. 1995. Effects of forest liming on soil processes. *Plant Soil* 168–169: 447–470.
- Kreutzer K. and Bittersohl J. 1986. Untersuchungen über die Auswirkungen des sauren Regens und der kompensatorischen Kalkung im Wald. *Forstw. Cbl* 105: 273–282.
- Kreutzer K., Göttlein A., Pröbstle P. and Zuleger M. 1991. Höglwaldforschung 1982–1989. Zielsetzung, Versuchskonzept, Basisdaten. *Forstwissenschaftliche Forschungen* 39: 11–21.
- Kreutzer K. and Weiss T. 1998. The Höglwald field experiment – aims, concept and basic data. *Plant Soil* 199: 1–10.
- Lindenmayer D.B. 1999. Future directions for biodiversity conservation in managed forests: indicator species, impact studies and monitoring programs. *Forest Ecology and Management* 115: 277–287.
- Lindenmayer D.B., Margules C.R. and Botkin D.B. 2000. Indicators of biodiversity for ecologically sustainable forest management. *Conservation Biology* 14: 941–950.
- Lindroth C.H. 1945. Die Fennoskanischen Carabidae. *Kungl. Vitterh. Samh. Handl. B4*. Göteborg, Sweden.
- Magura T., Tothmeresz B. and Bordan Z. 2000. Effects of nature management practice on carabid assemblages (*Coleoptera: Carabidae*) in a non-native plantation. *Biological Conservation* 93: 95–102.
- Magura T., Elek Z. and Tothmeresz B. 2002. Impacts on non-native spruce reforestation on ground beetles. *European Journal of Soil Biology* 38: 291–295.
- Magura T., Tothmeresz B. and Elek Z. 2003. Diversity and composition of carabids during a forest cycle. *Biodiversity and Conservation* 12: 73–85.
- Makeschin F. and Habereeder U. 1991. Einfluß von saurer Beregnung und Kalkung auf die Laufkäfer (Carabidae: Coleoptera) im Fichtenaltbestand Höglwald. *Forstwissenschaftliche Forschungen* 39: 128–134.
- Margi W.A. 1992. Faunistik der Sandlaufkäfer und Laufkäfer der Schweiz (Cicindelidae & Carabidae) Coleoptera unter besonderer Berücksichtigung der "Roten Liste". *Documenta Faunistica Helvetiae* 13. Centre suisse de cartographie de fauna, Neuchâtel, Switzerland.
- McCune B., Grace J.B. and Urban D.L. 2002. *Analysis of Ecological Communities*. MjM Software Design, Gleneden Beach, Oregon. ISBN 0-9721290-0-6. www.pcord.com
- Molnar T., Magura T., Tothmeresz B. and Elek Z. 2001. Ground beetles (Carabidae) and edge effects in oak-hornbeam forest and grassland transects. *European Journal of Soil Biology* 37: 297–300.
- Niemelä J., Langor D. and Spence J.R. 1993. Effects of clear-cut harvesting on Boreal ground beetle assemblages (Coleoptera: Carabidae) in Western Canada. *Conservation Biology* 7: 551–561.

- Poole A., Gormally M. and Skeffington M.S. 2003. The flora and carabid beetle fauna of a mature and regenerating semi-natural oak woodland in south east Ireland. *Forest Ecology and Management* 177: 207–220.
- Pretzsch H. 1996. Growth trends of forests in Southern Germany. In: Spiecker H., Mielikäinen K., Köhl M. and Skovsgaard J.P. (eds), *Growth Trends in European Forests*. European Forest Institute Report No. 5. Springer, Berlin, Heidelberg, New York, pp. 107–131.
- Rainio J. and Niemelä J. 2003. Ground beetles (Coleoptera: Carabidae) as bioindicators. *Biodiversity and Conservation* 12: 487–506.
- Röhle H. 1991. Entwicklung der wichtigsten ertragskundlichen Kenngrößen des Fichtenwaldbestandes Höglwald in der 6-jährigen Beobachtungsperiode 1983–1988. *Forstwissenschaftlichen Forschung* H. 39: 30–34.
- Rothe A., Huber C., Kreuzer K. and Weis W. 2002. Deposition and soil leaching in stands of Norway spruce and European beech: results from the Höglwald research in comparison with other European case studies. *Plant Soil* 240: 33–45.
- Rothe A. and Borchert H. 2003. *Der Wald von morgen. Eine Naturalbilanz über 25 Jahre naturnahe Forstwirtschaft im Bayerischen Staatswald*. LWF 39. Bayerische Landesanstalt für Wald und Forstwirtschaft, Munich, Germany.
- Thiele H.-U. 1977. *Carabid Beetles in Their Environment*. Springer, Berlin, Germany.
- United Nations 1992. *Agenda 21: the United Nations programme of action from Rio*. United Nations, New York.
- Werner S.M. and Raffa K.F. 2000. Effects of forest management practices on the diversity of ground-occurring beetles in mixed northern hardwood forests of the Great Lakes Region. *Forest Ecology and Management* 139: 135–155.