Biodiversity and Conservation (2007) 16:3653–3680
DOI 10.1007/s10531-006-9004-2
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The effect of femel- and small scale clear-cutting on ground dwelling spider communities in a Norway spruce forest in Southern Germany

CHRISTIAN HUBER*, CAROLINE SCHULZE 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 13 July 2005; accepted in revised form 30 January 2006

Key words: BACIP, Clear-cutting, Forest management, Höglwald, Selective-cutting, Species assemblage, Species-environment relationship, Spiders, Spruce

Abstract. The early effects of femel-cutting (removing 20% of the trees) and small scale clear-cutting on ground-living spiders in a Norway spruce (*Picea abies* (L.) Karst.) forest in Southern Germany were investigated. The study was carried out as BACIP (before and after, control-impact, many paired samplings) study: Spiders were sampled during the pre-treatment year, the year of cutting, and the year after cutting. In total 7101 individuals were sampled, of which 4530 individuals were identified, 4468 were adult and 2633 individuals were juvenile. We identified 107 species, but a single species, *Coelotes terrestris*, dominated the control (spruce stand) comprising up to 49% of the total identified individuals. Clear-cutting changed the species composition in the traps, while the first step in femel-cutting preserved it. The number of individuals of the families Linyphiidae, Amaurobiidae, Agelenidae and Clubionidae decreased drastically within the 2 years after the clear-cutting, while the Lycosidae became numerically dominant in the clear-cut stands. The number of individuals with the following characterisation decreased significantly after clear-cutting: Small (<3.0 mm) and large spiders (>10.5 mm), web builders, 'forest habitat species', species favouring hygrophilic to medium moisture conditions, and preferences to live below ground or in and on the moss layer. On the other hand, middle-sized spiders, free hunters, 'open habitat species', spiders favouring dry conditions or that are euryoecious, preferring patterns covered by grasses or uncovered patches, increased in number. Clear-cut habitats with dense spruce regeneration showed a delayed and less pronounced response. With femel-cutting, species composition of ground-living spider communities may be preserved during the first step of regeneration of mature forest stands.

Introduction

The Norway spruce stands in Southern Germany, which have largely replaced the original European beech forests, are well known by foresters for their high average annual volume increment (Huber et al. 2004a). However, recently concerns have arisen about possible negative ecological impacts of these uniform even-aged Norway spruce forests. These forests are highly susceptible to the frequent storm events, drought, and bark beetle outbreaks causing

unforeseen fellings, which increase the economic risks for forest managers (Anonymous 2004). Case studies made in some forests of this region show indications of serious ecological problems. Actual difficulties faced are the high nitrogen input (Huber and Kreutzer 2002; Huber et al. 2002; Rothe et al. 2002), soil acidification (Kreutzer 1995; Huber et al. 2004a), nitrate contamination of groundwater resources (Huber et al. 2004b; Rothe and Mellert 2004), and unexpectedly high N_2O emissions from the soils (Butterbach-Bahl et al. 1998). From a biodiversity perspective, these stands often appear uniform, and may have a low value for nature conservation.

One goal of the official forest management administration in Bavaria is to transform these pure coniferous stands into mixed forests. From 1987 to 2002, the proportion of areas with broadleaf trees increased from 22 to 32% (Anonymous 2004). In years to come, more and more conifer rich forests will be converted with efforts focused in the southern part of Bavaria. Therefore, we have studied exemplarily at the Höglwald site the impacts of regeneration on seepage water quality (Weis et al. 2001; Huber et al. 2004b), emission of nitrogen trace gases, and the diversity of different fauna groups before and in the first two years after the felling of the trees (for example Huber and Baumgarten 2005).

There are generally two methods used in this region for stand conversion. Either private forest owners make small clearcuts between 0.5 and 1 ha in size, or the Bavarian state forest administration regenerates the stands with femel cutting. Femel cutting is a relatively unspecific term for a cutting strategy to maintain a 'continuous covered forest'. Within a time span of 10–15 years single to groups of trees are selectively felled, while the saplings grow under the cover of the remaining stand. The final cutting will be done after the regeneration is established. With clear-cutting, the entire tree layer is removed causing an increase in temperature and decrease in shade (Geiger 1961).

The impacts, opportunities and threats of the two main management options on ecological important values are quite unclear and are, like many other forest practices, largely untested scientific hypotheses (Larsson and Danell 2001; Spence 2001; Siira-Pietikäinen et al. 2003). Femel-cutting or selective cutting is thought to have a lower impact on faunal groups and may serve as a potential tool for maintaining biodiversity in managed forests (Siira-Pietikäinen et al. 2003; Atlegrim and Sjöberg 2004; Huber and Baumgarten 2005). However, until now, studies on the ecological effects of femel-cutting are scarce. Also, data about the response of forest spiders are limited (Pajunen et al. 1995), despite the fact that spiders play a significant role as predators in forest ecosystems (Moulder and Reichle 1972; Buddle et al. 2000), are sensitive to habitat change (Robinson 1981; Riechert and Gillespie 1986; Uetz 1991), have clear taxonomic hierarchy (Duffey 1978), and are easily sampled and identified (Buddle et al. 2000).

In the paper we study the influence of two conversion methods (clear-cutting, femel-cutting) on spider communities. Our hypotheses are:

(I) Small-scale clear-cuts affect the assemblages of spiders:

  (a) Species richness increases due to the new structures of the small-scale clear-cut
  (b) The number of individuals of species typical for open habitats increases
  (c) The numbers of most forest species individuals decrease, but they are still present on the regeneration sites

(II) Femel-cutting preserves the original assemblages in the first cutting.

Materials and methods

Site description

The study was conducted at the Höglwald site, which has been a long-term ecological monitoring and experimentation site for more than 20 years with the focus on biogeochemistry and ecosystem research (Kreutzer and Bittersohl 1986; Kreutzer 1995; Butterbach-Bahl et al. 1998; Gessler et al. 1998; Kreutzer and Weiss 1998; Rothe et al. 2002; Huber et al. 2004a, b). The region belongs to the temperate broad-leaf zone, originally dominated by beech. The forest district of the Höglwald (370 ha) is situated in the hilly landscape of Southern Bavaria, 540 m above sea level, about 70 km north of the Alps and 50 km west of Munich (centre) at 11°04′ E and 48°17′ N. The forest is surrounded by intensively managed farmland (cattle breeding, diary, and corn). The climate is suboceanic. For the period 1984–2001 mean annual precipitation was 933 mm, mean annual temperature 7.7 °C, and the mean number of days exceeding 10 °C mean temperature was 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), which is strongly acidified in the topsoil. An organic layer 6–8 cm thick covers the mineral soil. The humus form is moder and the pH values are extremely low with a minimum in the Oh horizon of 2.75 (KCl). The investigated stands are healthy 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 spruce stand is growing vigorously with a high volume increment (Huber et al. 2004a), is full-stocked, and has a closed canopy. The last thinning was performed in 1975. Mosses dominate the ground vegetation.

Experimental treatments and plots

The experimental manipulations involved pre- and post-harvesting assessments. The study can be categorised as a BACIP (before and after, control-impact, many paired samplings) study. A great frequency of before and after

experimental designs are used in water studies and offer a practical alternative for studies where a treatment replication is not possible, but compensation for issues regarding spatial replication is needed (Bennett and Adams 2004). The benefits of these studies have been demonstrated recently in water and bio-diversity studies (Likens 2001; Siira-Pietikäinen et al. 2001, 2003; Huber et al. 2004a, b).

In 1999 the experimental plots were installed prior to the clear-cutting and femel-cutting treatments, which were performed with a harvester in February 2000. Stems including bark were removed and slash remained on the plots. In an area with very uniform stand and site conditions the following treatments were made:

C: control plot, spruce without cutting (named in other investigations A1)
F: femel-cutting (0.9 ha), regeneration with planted beech saplings
CC: small scale clear-cut (1.0 ha) divided into the following two parts
CCB: clear-cut, regeneration with planted beech saplings (0.5 ha)
CCS: clear-cut, regeneration with natural or planted spruce saplings (0.5 ha)

Femel-cutting was performed removing 20% of the trees in an area of approx. 0.9 ha, followed by planting beech saplings. The clear-cut was divided into 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, that originated from seedlings of the mature stand (natural regeneration). Fences and small roads separate the experimental treatments. The femel-cutting treatment is situated in the centre, 250 m NE is the control, and 150 m SE the clear-cut treatment.

Spiders were collected at each treatment (C, F, CCB, CCS) with a combination of pitfall (ten traps) and emergence traps (six traps), as was done previously in the study of Ratschker and Roth (2000) and Brand et al. (1994). Pitfall traps are commonly used for the collection of surface active animals, like spiders and beetles. The high number of species recorded, the continuous nature of the sampling, the easy and cheap handling and low maintenance favour the use of pitfall traps, despite some limitations (for discussion see Luff 1975; Uetz and Unzicker 1976; Curtis 1980; Phillips and Cobb 2005). Emergence traps (Bodenphotoeklektor Modell 250, ecotech GmbH, Bonn, Germany) were cone shaped tents without a bottom. The frame of the tent (ground surface 0.25 m^2) is worn in the humus layer, a pitfall trap is on the bottom, and on top of the tent a box is fixed containing coppersulphate (1%). The traps were established in each stand by placing them randomly close to the centre of each plot (ca. 10 m apart from each other), and close to other investigations made on the plots (for example elemental concentrations in seepage water, emission of trace gases, and meteorological measurements). At the small-scale clear-cut the distance between traps on CCB and on CCS and the distance to the nearest uncut stand was ca. 25 m. The trapping period covered most of the growing season (May–October) as recommended by Riecken (1999). 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 into 70% isopropanol and assigned to taxonomic

groups. Pitfall traps were plastic jars (diameter 75 mm, depth 100 mm) partly filled with ethyleneglycol. A transparent plastic roof (18 cm × 18 cm) was placed ca. 15 cm above the trap to prevent flooding from rainwater. Spider species were identified from the pitfall and emergence traps by a specialised expert (Helmut Stumpf, Würzburg, Germany), who also deposited the voucher specimens in his private collection. When species descriptions are based only on the genitalia, only sexually mature spiders were identified to species. Juvenile and penultimate stages were then only identified according to their genus or family. Some damaged individuals were unidentifiable. Besides spiders, numbers of individuals of other groups/families of animals were also counted. Collembola (separated into the groups Symphypleona and Entomobryomorpha), Carabidae (forest species and open habitat species according to Huber and Baumgarten 2005), Staphylinidae, Curculionidae, Elateridae, Isopoda, Gastropoda, Opiliones, Heteroptera and Myriapoda were used as environmental variables in the multivariate analyses (see Huber and Baumgarten 2005). The coverage of different species of ground vegetation close to the pitfall traps (2.0 m) was estimated for all years.

Photoactive radiation (PAR) was measured at 1 m height with a Licqor Par sensor. The measurements were used in detrended correspondence analysis (DCA; Hill and Gauch 1980 with corrections of Oksanen and Minchin, 1997), using the PC–ORD4 software package for windows (McCune et al. 2002). We first studied whether clear-cutting or femel-cutting affect the yearly catches of spider families in pitfall traps. We excluded from the analysis spider families with two or fewer individuals per plot and year. After these modifications we included in the analysis 19 environmental variables and 12 spider families. Second, we studied the effects of the treatments on total catches (pitfall + emergence traps) of the 20 dominant species. Referring to literature (Heydemann 1964; Jones 1990; Heimer and Nentweg 1991; Platen et al. 1991; Blick and Scheidler 2003) we made distinctions about size classes, ecology, and preferred habitat. Statistical analyses were performed with SPSS 11.5.1, SPSS Inc to study the effects of the treatments on the parameters size class, web, habitat, humidity preferences, stratum preference and stratum preference of ground dwellers for each year. Because all parameters were non-Gaussian distributed (Kolomogrov–Smirnov goodness of fit tests) and not equal in variance (Levene statistics), data were analysed using the non-parametric Kruskal–Wallis test. If significant differences among the treatments occurred, a multiple comparison was carried out with the non-parametric Mann–Whitney-*U*-test. The significance level used throughout was 5%.

Results

In total we sampled 7101 individuals (4468 adults and 2633 juveniles), of which 4530 individuals could be identified (Figure 1 and Appendix Table A1). The

number of individuals were highest in the pre-treatment year 1999 (Figure 1), while in the following years the number of individuals decreased. This was mostly due to the significantly higher number of individuals in 1999 during the first (May–June), and third (October) sampling period, while the numbers of individuals during the summer periods was not significantly different. The numbers of identified individuals were significantly lower at both clear-cut plots (CCB, CCS) in 2000 and 2001. In total 107 species of 16 families were identified with 70 species (35–44 species yearly) on the mature spruce plots (control plot, or plots before cutting, Figure 1) within 3 years of investigation. On the two clear-cut treatments 78 species were found after the cutting, with 63 species in 2000 (48 on CCB, 42 on CCS), and 45 species in 2001 (29 each on CCB and CCS). Fifteen species from seven families comprised more than 1% of the sample (printed in bold in Appendix Table A1). *Coelotes terrestris* was the dominant species with 1332 individuals followed by *Tapinocyba pallens* (615). Forty species appeared in all of the three investigation years with *Walckenaeria atrotibialis* the only species found every year on each plot. Linyphiidae and Amaurobiidae numerically dominated the control (Table 1). The first step in femel-cutting did not change the dominance of these two families. Individuals of the family Lycosidae, of which very few were collected before the clear-cut, dominated the clear-cut stand regenerated with beech in both years after the cutting. The clear-cut stand regenerated with spruce showed a delayed response compared to the beech regeneration plot, with Lycosidae dominating in the year after cutting (2001), but not in the year of cutting (2000).

Xerolycosa nemoralis was the only species that could be found exclusively on the clear-cuts, but not on the control or on the femel-cut. Only the Lycosidae *Pardosa lugubris*, *Trochosa terricola*, *Xerolycosa nemoralis*, and the Gnaphosidae *Zelotes clivicolus* were found in both clear-cut treatments after the cutting with two or more individuals. The most frequent spider species of the control were not collected after clear-cutting or decreased to very low values. The four most common species of the control, *Coelotes terrestris*, *Tapinocyba pallens*, *Coelotes inermis*, and *Agyneta ramosa* (all Linyphiidae or Amaurobiidae), were not collected in the year after clear-cutting on one of the clear-cuts and presented with only a few individuals at the other clearcut. *Tenuiphantes tenebricola* and *Gongylidiellum latebricola*, both Linyphiidae, were not collected in the year after the clear-cut. The number of individuals of Linyphiidae decreased after clear-cutting, but the family was still the second largest in number of individuals on the clear-cut plots until the end of the investigation.

Table 2 describes the changes of functional groups before and after cutting (see Appendix Table A1 for classification). The size distribution of spiders changed after clear-cutting. The number of individuals from the smallest size class 1 (0–3 mm) and the biggest size class 4 (>10.5 mm) decreased, whereas the number of individuals in size class 3.0–10.5 mm increased (Table 2). The number of individuals of web building spiders dramatically decreased after the clear-cut. Funnel web spiders (Agelenidae) were totally absent on the clear-cut in the year after the cutting. Also very few hackledmesh weavers (Amaurobiidae)

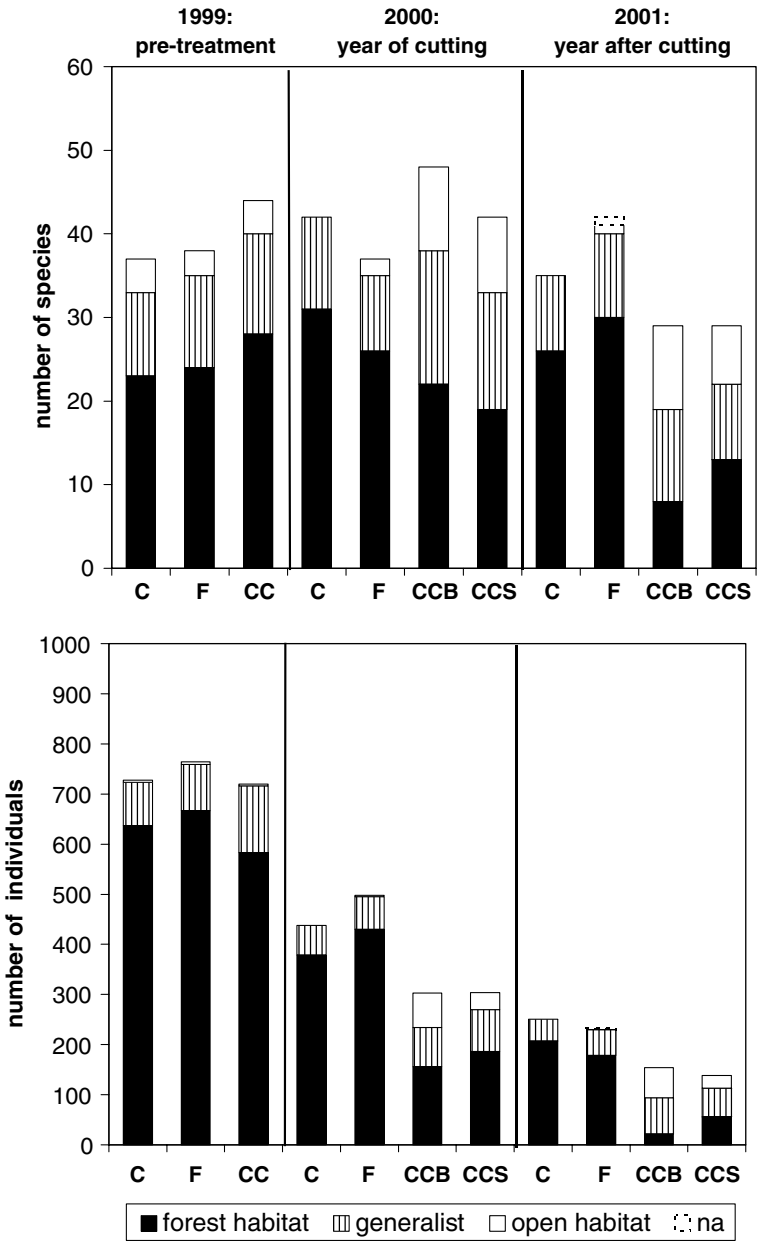

Figure 1. Total number, number of forest habitat, generalists, and open habitat spider species (above), and identified individuals (below), in 1999 (pre-treatment year), 2000 (year of cutting), and 2001 (year after the cutting) for each treatment. C = control, F = femel, CC = clear-cut, CCB = clear-cut beech, CCS = clear-cut spruce.

Table 1. Percentage of number of individuals of spider families for each treatment in the sampling years 1999 (pre-treatment year), 2000 (year of cutting) and 2001 (year after cutting).

Family	1999			2000				2001			
	C	F	CC	C	F	CCB	CCS	C	F	CCB	CCS
Agelenidae	2	1	1	2	2	0	0	2	3	0	0
Amaurobiidae	41	47	39	48	48	10	36	40	31	4	14
Araneidae	0	0	0	0	0	0	2	1	0	0	0
Clubionidae	1	0	1	0	0	0	0	5	2	0	1
Dictynidae	2	2	3	0	1	0	1	4	5	1	2
Dysderidae	0	0	0	0	0	0	0	0	0	0	0
Gnaphosidae	0	0	0	0	0	2	3	0	0	3	11
Hahniidae	0	1	4	0	0	1	5	0	2	0	9
Linyphiidae	50	46	45	42	46	19	39	40	48	13	20
Lycosidae	0	0	3	2	0	66	9	1	2	64	37
Philodromiidae	0	0	0	1	1	0	1	1	0	0	1
Salticidae	0	1	1	1	0	0	1	1	1	2	1
Segestriidae	0	0	0	0	0	0	0	1	2	0	0
Tetragnatidae	0	0	0	0	0	0	0	1	0	2	1
Theridiidae	1	1	1	2	0	1	2	2	1	1	2
Thomisidae	1	1	2	1	2	0	2	2	3	9	2

Treatment: C = control, F = femel, CC = clear-cut, CCB = clear-cut beech, CCS = clear-cut spruce.

were collected on the clear-cut plots (Table 1). Nearly all Amaurobiidae collected on the clear-cuts were juvenile, while adult species were absent.

Within the year after clear-cutting a significant increase took place in the total number of open habitat species, mostly free hunting spiders like Lycosidae and Thomisidae (Table 1). The number of individuals of forest species decreased significantly after clear-cutting from the year of cutting to the year after cutting. There was no significant effect in this parameter by femel-cutting. After clear-cutting the number of individuals that are hygrophilic or favour medium moisture conditions decreased, while increases were exhibited in the number of individuals favouring dry conditions (xerophilous), or that are independent (euryoecious) in relation to moisture. On the control plot hygrophilic individuals were much lower in the years 2000 and 2001 compared with 1999, while the number of individuals with middle moisture preferences was much lower in 2001 than in previous years.

The number of individuals living preferentially below the ground decreased drastically after clear-cutting. The fraction of individuals preferring an uncovered habitat on the ground or grass mulch increased, while individuals preferring a humus layer with mosses decreased.

Figure 2 describes the results of DCA analysis of the total catches (pitfall traps + emergence traps) of the 20 most numerous spider species in the different years and treatments. The mature spruce plots (CCB, and CCS in the pre-treatment year, and plot C in all three years) together with the femel-cut

Table 2. Average number of identified individuals per trap (emergence + pitfall traps) with standard error attributed to the parameters: habitat fixation, size class, web, humidity preference, stratum preference, and stratum preference of ground dwellers according to the data in Appendix Table A1.

Parameter		1999			2000				2001			
		C	F	CC	C	F	CCB	CCS	C	F	CCB	CCS
Total	Adult	45.5 ± 3.5 a	47.8 ± 3.6 a	45.0 ± 3.8 a	27.4 ± 4.2 ab	31.1 ± 3.6 a	20.2 ± 1.7 b	19.0 ± 1.5 b	15.7 ± 2.1 a	14.5 ± 1.5 a	9.6 ± 1.1 b	9.2 ± .1.4 b
Size class	< 3 mm	23.4 ± 2.8 a	23.8 ± 4.5 a	24.9 ± 3.0 a	11.6 ± 1.7 a	12.7 ± 1.0 a	9.2 ± 1.3 a	10.1 ± 1.4 a	8.2 ± 1.2 a	7.4 ± 1.3 a	2.7 ± 0.4 b	3.9 ± 0.9 b
	> 3–10.5 mm	3.1 ± 0.4 a	1.8 ± 0.4 b	4.4 ± 0.6 a	2.1 ± 0.5 c	2.3 ± 0.3 c	8.9 ± 1.0 a	4.8 ± 0.7 b	2.9 ± 0.4 c	3.3 ± 0.6 bc	6.9 ± 0.9 a	4.7 ± 0.8 ab
	> 10.5 mm	18.9 ± 4.1 a	22.1 ± 4.1 a	15.6 ± 3.1 a	13.6 ± 3.1a	16.2 ± 3.2 a	2.1 ± 0.5 c	4.0 ± 0.7 b	4.6 ± 1.3 a	3.6 ± 0.9 a	0.0 ± 0.0 c	0.6 ± 0.3 b
Web	No web	1.1 ± 0.3 b	0.9 ± 0.3 b	3.1 ± 0.5 a	0.8 ± 0.3 c	0.4 ± 0.2 c	8.4 ± 0.9 a	4.2 ± 0.7 b	0.9 ± 0.2 c	1.0 ± 0.3 c	6.9 ± 0.7 a	4.6 ± 0.7 b
	Web	44.4 ± 3.5 a	46.8 ± 3.6 a	41.9 ± 3.5 a	26.6 ± 4.2 a	30.8 ± 3.5 a	11.8 ± 1.4 b	14.8 ± 1.3 b	14.8 ± 2.1 a	13.5 ± 1.6 a	2.7 ± 0.5 b	4.6 ± 1.0 b
Habitat fixation	Open habitats	0.3 ± 0.2 a	0.2 ± 0.1 a	0.3 ± 0.1 a	0.0 ± 0.0 c	0.1 ± 0.1 c	5.0 ± 0.6 a	2.3 ± 0.5 b	0.0 ± 0.0 c	0.0 ± 0.0 c	3.9 ± 0.6 a	1.9 ± 0.4 b
	Generalist	5.3 ± 0.5 a	5.6 ± 1.2 a	8.3 ± 2.1 a	3.8 ± 0.6 a	4.1 ± 1.0 a	4.9 ± 0.6 a	5.2 ± 0.7 a	2.8 ± 0.4 a	3.3. ± 0.5 a	4.4 ± 0.7 a	3.5 ± 0.9 a
	Forest habitats	39.9 ± 3.2 a	42.0 ± 3.5 a	36.5 ± 2.6 a	23.6 ± 3.9 a	26.9 ± 3.7 a	10.3 ± 1.4 b	11.6 ± 1.1 b	12.9 ± 1.9 a	11.2 ± 1.4 a	1.4 ± 0.4 b	3.7 ± 1.0 b
Humidity preference	Hygrophil	23.0 ± 2.0 a	23.4 ± 2.9 a	23.8 ± 2.6 a	8.0 ± 1.3 a	9.1 ± 1.2 a	6.9 ± 1.0 a	7.8 ± 1.1 a	7.2 ± 1.2 a	6.5 ± 0.8 a	2.1 ± 0.3 b	2.8 ± 0.7 b
	Mid humid/dry	18.7 ± 3.2 ab	21.8 ± 2.7 a	13.3. ± 2.0 b	15.5 ± 3.2 a	18.8 ± 2.7 a	3.0 ± 0.7 c	4.8 ± 0.6 b	4.9 ± 0.8 a	4.9 ± 0.8 a	0.2 ± 0.1 b	0.6 ± 0.2 b
	Euryoecious	0.3 ± 0.2 a	0.2 ± 0.1 a	0.3 ± 0.2 a	0.2 ± 0.1 c	0.1 ± 0.1 c	4.0 ± 0.5 a	1.5 ± 0.4 b	0.7 ± 0.2 b	0.6 ± 0.2 b	2.3 ± 0.4 a	0.7 ± 0.3 b
	Xerophil	3.5 ± 0.7 b	2.4 ± 0.6 b	7.6 ± 0.8 a	3.8 ± 0.7 ab	3.2 ± 0.7 b	5.9 ± 0.9 a	4.9 ± 0.6 a	2.9 ± 0.5 b	2.4 ± 0.4 b	5.2 ± 0.7 a	4.8 ± 0.8 a
Stratum preference	Underground	10.0 ± 2.1 a	11.4 ± 2.1 a	8.1 ± 1.6 a	7.2 ± 1.6 a	8.5 ± 1.7 a	1.2 ± 0.3 b	2.0 ± 0.3 b	2.7 ± 0.7 a	2.2 ± 0.5 a	0.0 ± 0.0 c	0.3 ± 0.1 b
	Ground-dwelling	31.8 ± 2.1 a	32.5 ± 3.0 a	30.2 ± 2.7 a	16.8 ± 2.4 a	19.6 ± 2.0 a	16.6 ± 1.5 a	14.4 ± 1.5 a	8.9 ± 1.0 a	8.6 ± 0.8 a	7.5 ± 0.9 a	7.4 ± 1.3 a
	Above-ground	3.4 ± 0.5 b	3.8 ± 0.8 b	6.7 ± 0.8 a	2.9 ± 0.6 a	3.0 ± 0.4 a	2.4 ± 0.6 a	2.6 ± 0.5 a	4.1 ± 0.8 a	3.6 ± 0.9 a	2.1 ± 0.3 b	1.5 ± 0.4 b
Stratum preference of ground dwellers	Uncovered	0.0 ± 0.0 a	0.0 ± 0.0 a	0.0 ± 0.0 a	0.0 ± 0.0 b	0.0 ± 0.0 b	0.3 ± 0.1 a	0.2 ± 0.1 a	0.0 ± 0.0 b	0.0 ± 0.0 b	0.8 ± 0.3 a	0.3 ± 0.2 a
	Moss	12.3 ± 1.0 a	10.5 ± 1.5 ab	9.2 ± 0.9 b	5.1 ± 0.9 a	5.5 ± 0.7a	2.3 ± 0.3 b	2.9 ± 0.3 b	2.3 ± 0.3 a	1.8 ± 0.2 a	0.6 ± 0.2 b	0.9 ± 0.5 b
	Litter	16.5 ± 1.3 a	18.5 ± 1.4 a	16.9 ± 1.3 a	9.3 ± 1.4 ab	11.1 ± 1.4 a	6.8 ± 0.9 b	7.1 ± 0.9 ab	4.9 ± 0.7 ab	5.0 ± 0.6 a	3.3 ± 0.4 b	4.0 ± 0.8 ab
	Grass	2.5 ± 0.2 a	3.1 ± 0.6 a	3.8 ± 0.7 a	2.1 ± 0.3 c	2.6 ± 0.4 bc	6.5 ± 0.7 a	3.3 ± 0.5 b	1.2 ± 0.2 b	1.6 ± 0.2 b	2.7 ± 0.4 a	1.7 ± 0.4 ab

Sampling years: pre-treatment year (1999), year of cutting (2000), and year after the cutting (2001). Treatments: C = control, F = femel, CC = clear-cut, CCB = clear-cut beech, CCS = clear-cut spruce. Different letters indicate a statistically significant ($p < 0.05$) difference between the treatments for each investigated year.

plot (F) are clearly separated from the clear-cut plots CCB and CCS after the felling. Factors reflecting clear-cut conditions (higher radiation, precipitation, and number of individuals of open habitat Carabidae) were on the optimum right of the origin. Factors reflecting dense forest conditions (for example: coverage of mosses, forest species of Carabidae, Curculionidae, Staphylinidae) were on the optimum left of the origin. One 'forest and open habitat' species (the Linyphiidae *Gongylidiellum latebricola*), and six forest species (the Linyphiidae *Tenuiphantes tenebricola*, *Tapinocyba pallens* and *Walckenaeria alticeps*, the Agelenidae *Histopona torpida*, and the Amaurobiidae *Coelotes terrestris* and *Coelotes inermis*) are clustered left of the origin of the ordination together with the untreated or femel stands. The number of individuals of these species drastically decreased (or were totally absent) on the clear-cut in the year of cutting (2000) and after the cutting (2001). 'Open habitat' or 'forest and open habitat' (generalist) species were clustered on the right side of the ordination, together with the clear-cut plots. The Lycosidae *Xerolycosa nemoralis*,

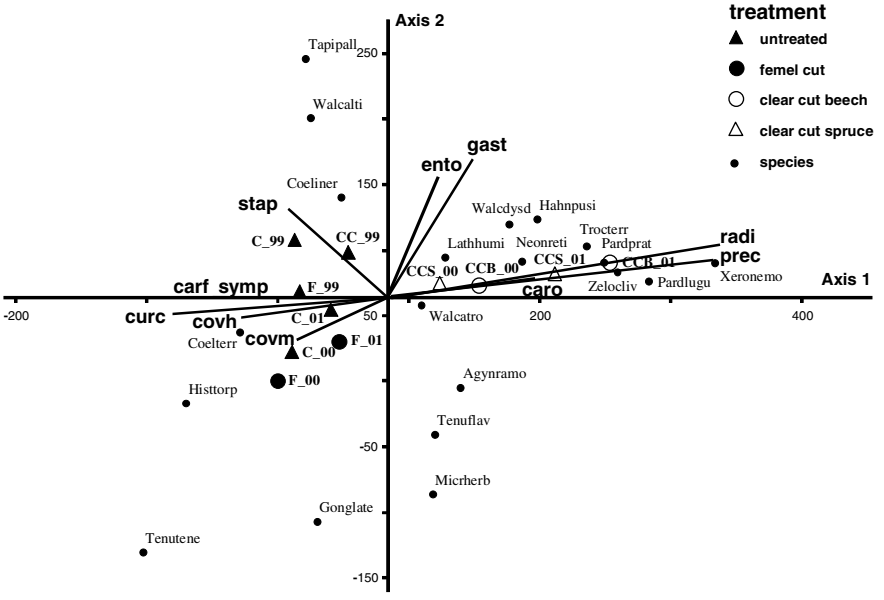

Figure 2. DCA ordination of the 20 most numerous species in the different treatments for the total catch of pitfall and emergence traps. _99 = year 1999 (pre-treatment year), _00 = year 2000 (year of cutting), _01 = year 2001 (year after cutting). Treatments: C = control, F = femel, CCB = clear-cut beech, CCS = clear-cut spruce. All plots within the pre-treatment year and the control plot are marked as 'Untreated'. The eight-letter abbreviations indicate the species, e.g. Coelterr = *Coelotes terrestris*. Abbreviations of the species are listed in Appendix Table A1. Lable explanations: gast = number of individuals of Gastropoda, ento = Entomobryomorpha, symp = Symphypleona, curc = Curculionidae, stap = Staphylinidae, carf = Carabidae of forest habitats, caro = Carabidae of open habitats, prec = precipitation, radi = photosynthetic active radiation, covh = coverage of herbs, covm = coverage of mosses.

Pardosa lugubris, *Pardosa prativaga*, *Trochosa terricola* and the Gnaphosidae *Zelotes clivicolus* were nearly absent in the spruce stand before, but were favoured by clear-cutting. The species *Neon reticulatus*, *Hahnia pusilla*, *Walckenaeria dysderoides* and *Lathys humilis* showed (1) no clear effect of treatment, (2) strong year-to-year fluctuations, or (3) pre-treatment differences. Three species (all Linyphiidae), *Walckenaeria atrotibialis*, *Agyneta ramosa*, *Micrargus herbigradus*, right of the origin and below axis 1 showed a delayed response of the clear-cut treatment with a clear effect only in 2001.

The multivariate analyses from all pitfall traps with the spider families showed the following results (Figure 3a, b). Nearly all pitfall traps from the femel-cutting and the control plot were clustered left of the centre. Traps from the clear-cut plots are separated from these traps. Traps from the CCS plot showed a delayed response, indicating that most of the traps were close to the control traps in the year of cutting, but were clearly separated in the year after the cutting. The families Amaurobiidae, Clubionidae, Agelenidae, and Linyphiidae were clustered on the left side of the centre. The Lycosidae were close to the vectors precipitation and radiation, which indicate clear-cut conditions.

Discussion

The number of individuals in the control decreased from 1999 to 2001. The reasons for this decrease are unclear. One can assume that this decrease may be the effect of repeating sampling. However, summer sampling data were very similar for all years. Also, climatic factors may be responsible for the difference between years. For example, in the year 2000 the decrease was restricted to individuals with a hygrophilic humidity preference (see Table 2). This finding is in good agreement with a very dry period during the first sampling period in June 2000, while 1999 was characterised with heavy rainfall during this period. September 1999 was the warmest September of the century, but with enough rain. These climate conditions may be responsible for the high number of individuals sampled in autumn 1999. The year 2001 was characterised by a soil frost at the beginning of the year, which is very unusual on this site and a long winter period until April. The first sampling period was first very dry and hot, followed by heavy rain. This climatic situation may be reflected in the lower number of individuals (1) with stratum preference 'underground', and (2) hygrophilic to mid humid/dry humidity preferences (see Table 2).

The number of species of the investigated even-aged spruce stand at the Högwald is in the range of more natural beech forests in Southern Germany (Dumpert and Platen 1985; Brand et al. 1994). The dominant families at our site were Linyphiidae and Amaurobiidae. This was also reported in other investigations of deciduous and coniferous stands in southern Germany (Brand et al. 1994; Engel 1999; Junker et al. 2000). Linyphiidae also dominated in Scots and Lodgepole pine stands in Scotland (Docherty et al. 1997), in coniferous stands in southern Finland (Pajunen et al. 1995), with Agelenidae

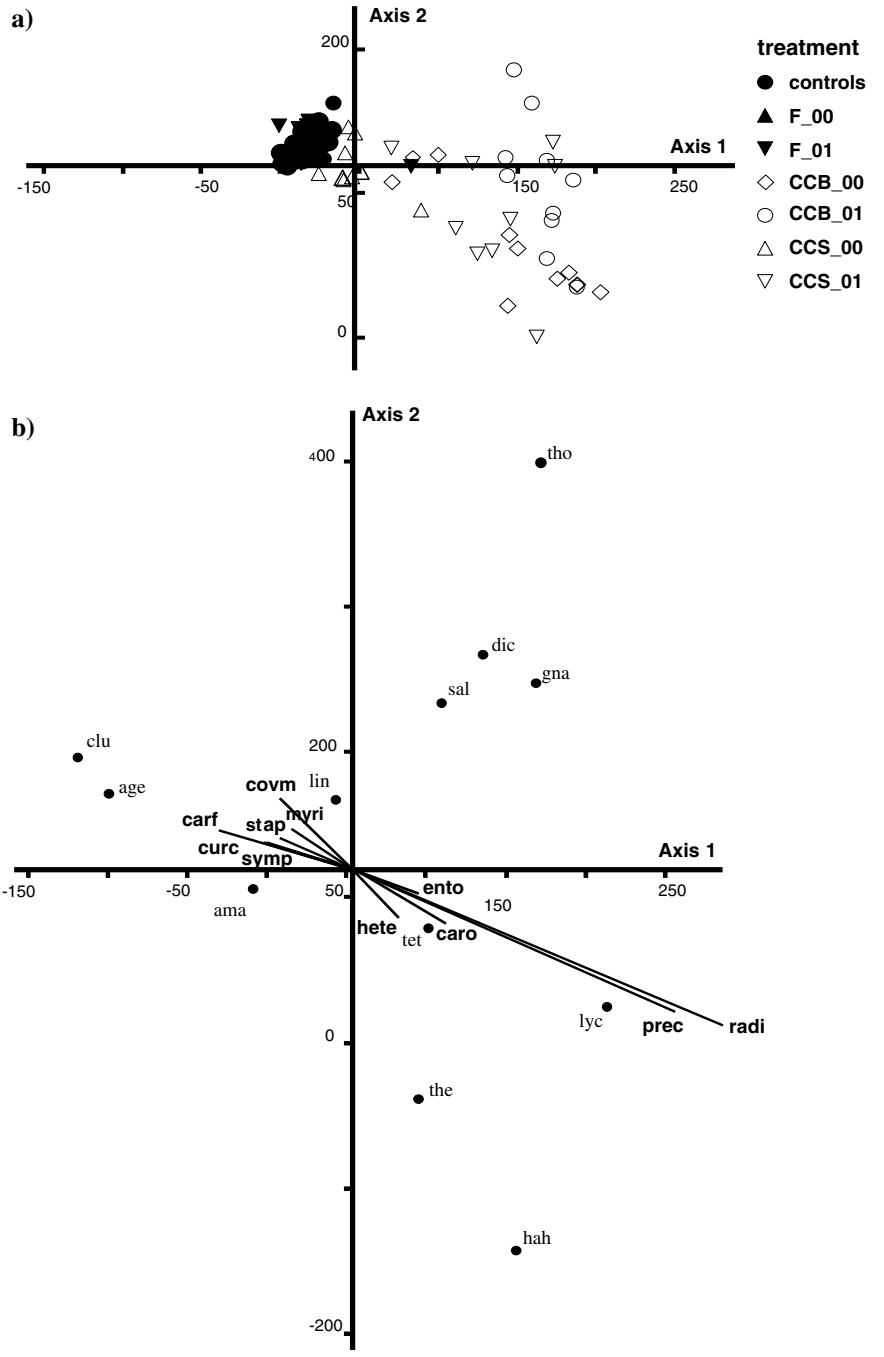
a)
Axis 2
Axis 1
200
0
-150
-50
50
150
250
treatment
controls
F_00
F_01
CCB_00
CCB_01
CCS_00
CCS_01
b)
Axis 2
Axis 1
400
200
-200
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Figure 3. (a) DCA ordination for single pitfall traps for the years 1999 (pre-treatment), 2000 (year of cutting) and 2001 (year after cutting). (b) DCA ordination of the twelve most numerous families sampled during 1999–2001. The three-letter abbreviations indicate the families, e.g. Lin = Linyphiidae. Abbreviations of the spider families are listed in Appendix Table A1. 'Controls' are all pitfall traps from the pre-treatment year and of the control in 2000 and 2001. _00 = year 2000, _01 = year 2001. F = femel, CCB = clear-cut beech, CCS = clear-cut spruce. Lable explanations: ento = number of individuals of Entomobryomorpha, symp = Symphypleona, curc = Curculionidae, stap = Staphylinidae, hete = Heteroptera, caro = Carabidae of open habitats, carf = Carabidae of forest habitats, myri = Myriapoda, prec = amount of precipitation, radi = yearly photosynthetic active radiation, covm = coverage of mosses.

in an 'old growth' coniferous forest in Oregon, USA. (McIver et al. 1992), and with Amaurobiidae and Agelenidae in a dense spruce fir forest of Maine, USA (Jennings et al. 1988). Lycosidae were absent or scarce in our spruce stand and in other mature forests (Bultman et al. 1982; Jennings et al. 1988; Brand et al. 1994). In contrast to these results, Lycosidae were the dominant family in a study of mature boreal forests (aspen, mixed wood, and spruce) in Canada (Pearce et al. 2004). However, in this study the stands had open canopies with an average tree cover of only 12–20%.

Spider assemblages responded quickly within the year of clear-cutting in our experiment as in the investigation of Buddle et al. (2000) after wildfire and clear-cutting. While the total number of species was more or less unaffected, the number of forest habitat species decreased, and the number of open habitat species increased. After clear-cutting, free hunting spiders (mostly Lycosidae) were favoured in our study. This guild is more mobile than web builders and therefore has a greater flexibility (Pearce et al. 2004). The increase of Lycosidae and the decrease of Linyphiidae in our study following clear-cutting have also been reported by other studies in different regions of the world (Huhta 1971; Coyle 1981; Curry et al. 1985; Jennings et al. 1988; McIver et al. 1992; Pajunen et al. 1995; Atlegrim and Sjöberg 1995; Pearce et al. 2004).

After the clear-cutting, we observed a distinct increase of Gnaphosidae (mainly *Zelotes clivicoles*). This was also the case after clear-cutting in coniferous forests of Finland (Pajunen et al. 1995). The Gnaphosidae prefer nearly exclusively the clear-cut habitat in our study, as in the study of Buddle et al. (2000), where *Gnaphosa borea* was exclusively discovered in fire-originated stands.

After clear-cutting a dramatic decrease in the number of spiders with habitat preferences 'below the ground' (for example in the humus layer) or of species preferring the moss layer took place (see also Siira-Pietikäinen et al. 2003). Spiders react preferentially to abiotic factors like humidity, temperature, and light (Huhta 1971; Platen et al. 1991). Tree species, mixtures of tree species, dead wood or microhabitat attributes seem to be of lower importance (Platen et al. 1991; Engel 1999; Pearce et al. 2004) compared to tree cutting procedures. Therefore one can assume that the decrease of 'underground species' on the clear-cuts can be explained with an increase in maximum and average temperature in the uppermost sub-layers of the humus layer during summer.

Furthermore, these layers were periodically drier at the clear-cut than at the control. After clear-cutting, the humus layer became thinner due to an increase in mineralisation and a decrease in litter fluxes due to the absence of the mature stand. Only free hunting spiders like the Lycosidae were favoured under such conditions because they are typical field inhabitants, best suited for locomotion in habitats where little litter accumulates, or were litter has been removed (Uetz 1979; Bultman et al. 1982). The decrease of spiders with moss habitat preferences corresponds well with the decrease in coverage of mosses after clear-cutting as a result of a higher light intensity.

Our results of the DCA analysis indicate that Agelenidae and Amaurobiidae prefer the very dense parts of the spruce forest at the Höglwald site, which have not been thinned for some decades. After clear-cutting the Amaurobiidae decreased dramatically in our experiment, as well as after a wind throw of a beech forest in southern Germany (Brand et al. 1994). Linyphiidae also preferred the forest interior, but some species were also numerous in the clear-cuts. Linyphiidae inhabit complex microhabitats in the leaf litter and soil of forests (Huhta 1971; Buddle et al. 2000), but they are also believed to survive harvesting by moving deep into the litter (Buddle et al. 2000). Besides a low heat tolerance, the decrease in ground cover of shrubs following clear-cutting should decrease the opportunity to spin webs and lower the habitat quality for this spider group (Huhta 1971; Atlegrim and Sjöberg 1995). However, at the mature spruce stand at the Höglwald site nearly no shrubs were present before the cutting. On the contrary, a new structure was established with planting of the spruce and beech saplings. In our femel-cutting treatment the spider fauna did not significantly differ from that in the untreated spruce stand (Atlegrim and Sjöberg 1995) despite the fact that some new structures were generated after the felling (beech sapling layer, tree stumps, branches left on the site, etc.).

Clear-cut habitats are more heterogeneous in two dimensions (Huber and Baumgarten 2005; Pearce et al. 2004) with water filled ruts, uncovered microhabitats, different vegetation structures and so on. Nevertheless, the number of species on the clear-cut plots was not higher in the year after cutting (2001) than in the pre-treatment period, or on the control or femel-cut. Coyle (1981), Atlegrim and Sjöberg (1995), and Buddle et al. (2000) also found fewer numbers of individuals after clear-cutting, while more individuals of spiders were collected after a wind throw in Germany (Brand et al. 1994) or in clear-cuts in Canada (Pearce et al. 2004) compared to the control.

Collembola are regarded as the most important prey of small spiders, owing to their abundance, appropriate size (0.2–5 mm), thin integument and relative defencelessness (Huhta 1971). The number of Collembola (mainly Entomobryomorpha) increased enormously after clear-cutting at the Höglwald site (data not shown) or in other experiments (Huhta et al. 1967, 1969). However, the total number of adult spiders did not show this same trend. Huhta et al. (1967) also observed no increase in the spider populations after a fertiliser-induced increase of Collembola. The number of potential prey animals seems not to influence the size of spider populations (Kajak 1965; Turnbull 1966; Huhta 1971).

Forest spiders may recover relatively rapidly after disturbances, when there is a possibility to rebuild the communities from uncut stands. Huhta (1971) found that forest spider assemblages began resembling those of an old pine/spruce forest between 7 and 13 years after burning and clear-cutting. After around 15 years of forest growth web building forest species became increasingly dominant (Buddle et al. 2000), with succession of the forest toward canopy closure (Huhta 1971) and a recovery of the spider assemblages was apparent 30 years after clear-cutting (McIver et al. 1992).

Conclusions

The untreated homogenous Norway spruce stands at the Höglwald site exhibited a relatively high diversity of spider species. The spider community exhibited a fast and pronounced change in species composition after clear-cutting, which is clearly reflected in the ecological demands of the newly occurring species on the clear-cut. If the forest spider species of mature stands should be preserved during the regeneration process in the hope that this group best fulfils the functionality of the system, femel-cutting should be favoured. The final cutting in this long lasting process should be done after a dense regeneration has been established. This procedure will also help to reduce the risk of nitrate leaching (see Huber et al. 2004b). A dense natural or planted regeneration before clear-cutting may also help to preserve the original community due to the shading effect, or at least help to slow down the effects of clear-cutting on forest species. Indications from literature are given that even in clear-cuts a typical forest species community of spiders will be re-established after approx. 30 years. As a requirement, enough areas of dense mature stands in the forest should be left as retreats for the forest species. Long-term investigations are needed to give more information about species composition after femel- and clear-cutting, also taking into account periods of a possible return of forest species in later years. However, such investigations are still rare in ecological research due to the pattern of funding for research (Tilman, 1989). Further, investigations on various sites are needed, which compare the regeneration methods in the region to give more insight about the heterogeneity/diversity of spiders on a landscape scale.

Acknowledgements

The work was funded by the Bundesministerium für Bildung, Forschung und Technologie (BMBF), under contract number 0339733A. The authors are very grateful to Helmut Stumpf, Würzburg, Germany for the identification of spider species and the safekeeping of the specimens. We thank Dr Jacquie van der Waals, University of Pretoria, for editing of the manuscript and two anonymous reviewers for their comments to improve the manuscript.

Appendix A.

Table A1. Number of individuals of identified species and corresponding ecological parameters size class (SC), web, habitat (HAB), moisture demand (MD), and stratum (STR) for each treatment in 1999 (pre-treatment year), 2000 (year of cutting), and 2001 (year after cutting).

Family	Species	Abbr.	1999			2000				2001				∑	SC	Web	HAB	MD	STR
			C	F	CC	C	F	CCB	CCS	C	F	CCB	CCS						
Agelenidae (Age)	***Histopona torpida* (C.L. KOCH, 1834)**	*Histtorp*	16	9	8	13	11	1	0	9	10	0	0	77	3	1	F	h	0–11
Amaurobiidae (Ama)	*Amaurobius fenestralis* (STROEM, 1768)		0	0	1	1	0	0	0	7	8	0	0	17	3	1	F	eu	0–2
	Amaurobius ferox (WALCKENAER, 1830)		1	0	0	0	0	0	0	0	0	0	0	1	4	1	O	x	0–1g
	Amaurobius sp.		1	1	0	0	0	0	0	0	0	0	0	2	–	–	–	–	–
	***Coelotes inermis* (L. KOCH, 1855)**	*Coeliner*	49	63	76	13	16	7	9	25	21	0	5	284	4	1	F	h	0–1l
	Coelotes sp.		54	95	99	79	91	74	148	67	33	12	25	777	–	–	–	–	–
	***Coelotes terrestris* (WIDER, 1834)**	*Coelterr*	251	291	174	204	243	25	55	48	37	0	4	1332	4	1	F	mid	0–1l,m
Araneidae (Ara)	Araneidae sp.		0	0	0	1	1	0	6	1	0	0	0	9	–	–	–	–	–
	Araneus angulatus (CLERCK, 1757)		1	0	0	0	0	0	0	0	0	0	0	1	4	1	F	h	2
	Araneus sturmi (HAHN, 1831)		0	0	0	0	0	0	2	1	0	1	0	4	2	1	F	x	2
	Cyclosa conica (PALLAS, 1772)		0	0	1	0	0	0	0	0	0	0	0	1	3	1	F	x	2
	Gibbaranea sp.		0	0	0	0	1	0	0	0	0	0	0	1	–	–	–	–	–

	Mangora acalypha (WALCKENAER, 1802)		0	0	0	0	0	0	1	0	0	0	0	1	2	1	O	x	2
Clubionidae (Clu)	*Clubiona marmorata* (L.KOCH, 1866)		0	0	0	0	0	0	0	0	1	0	0	1	na	0	F	n.a.	2
	Clubiona sp.		1	1	3	0	0	0	0	11	1	0	0	17	–	–	–	–	–
	Clubiona subsultans (THORELL, 1875)		2	0	0	0	2	0	0	5	4	0	2	15	3	0	F	x	1m-2
	Clubiona terrestris (WESTRING, 1862)		9	1	7	2	0	0	0	1	1	0	0	21	3	0	G	x	1l,g
Dictynidae (Dic)	*Cicurina cicur* (FABRICIUS, 1793)		6	8	5	1	3	1	1	0	0	1	0	26	3	1	G	mid	0-1l-2
	***Lathys humilis* (BLACKWALL, 1855)**	*Lathhumi*	13	10	20	2	1	0	4	15	17	2	4	88	1	1	F	mid	1l,g-2
Dysderidae (Dys)	*Harpactea lepida (C.L. KOCH, 1939)*		0	0	1	2	0	5	1	1	0	0	0	10	3	0	F	h	1l
Gnaphosidae (Gna)	***Zelotes clivicolus* (L. KOCH, 1870)**	*Zelocliv*	1	1	3	2	0	21	18	0	1	8	23	78	2	0	F	x	1l
	Zelotes sp.		0	0	0	0	0	0	0	0	0	3	2	5	–	–	–	–	–
Hahniidae (Hah)	*Cryphoeca silvicola* (C.L. KOCH, 1834)		0	0	0	1	0	3	0	0	0	0	0	4	1	1	F	h	0–1l
	***Hahnia pusilla* (C.L. KOCH 1841)**	*Hahnpusi*	0	7	39	0	2	3	25	0	5	0	22	103	1	1	G	h	1l,g,m
	Hahnia sp.		0	0	0	0	0	0	4	0	0	0	0	4	–	–	–	–	–
Linyphiidae (Lin)	*Agyneta conigera* (O.P.- CAMBRIDGE, 1863)		0	0	2	0	0	0	1	0	1	0	1	5	1	1	F	h	1l
	***Agyneta ramosa* (JACKSON, 1912)**	*Agynramo*	15	42	22	20	33	30	17	6	6	1	0	192	1	1	F	h	1l,g
	Asthenargus helveticus (SCHENKEL, 1936)		0	4	0	3	3	2	9	2	0	0	2	25	1	1	G	h	1
	Bathyphantes nigrinus (WESTRING, 1851)		0	0	0	0	0	1	0	0	0	0	0	1	1	1	F	h	1l-2

Table A1. Continued.

Family	Species	Abbr.	1999			2000				2001				∑	SC	Web	HAB	MD	STR
			C	F	CC	C	F	CCB	CCS	C	F	CCB	CCS						
	Bathyphantes parvulus (WESTRING, 1851)		0	0	0	0	0	1	0	0	0	0	0	1	1	1	O	eu	1l,g-2
	Centromerus aequalis (C.L. KOCH, 1841)		0	8	8	0	2	0	0	0	2	0	0	20	1	1	F	h	1l
	Centromerus arcanus (O.P.-CAMBRIDGE, 1873)		0	0	0	0	0	2	0	0	0	0	0	2	1	1	O	h	1m
	Centromerus incilium (L.KOCH, 1881)		0	0	0	1	0	0	0	0	1	0	0	2	1	1	F	x	1l,m
	Centromerus pabulator (O.P.-CAMBRIDGE, 1857)		1	1	5	0	2	0	0	0	5	1	0	15	2	1	G	x	1l,g
	Centromerus sylvaticus (BLACKWALL, 1841)		0	0	0	0	0	0	0	0	1	0	2	3	2	1	F	h	1l,g-2
	Ceratinella brevis (WIDER, 1834)		3	3	2	1	0	1	0	2	2	0	1	15	1	1	F	h	1l,g
	Ceratinella scabrosa (O.P.-CAMBRIDGE, 1871)		0	5	6	0	1	1	15	0	0	0	0	28	1	1	F	h	1l
	Dicymbium cf *brevi-setosum* (LOCKET, 1962)		1	0	0	0	0	0	0	0	0	0	0	1	na	1	O	eu	1
	Diplocephalus latifrons (O.P.-CAMBRIDGE, 1863)		1	3	0	0	0	0	0	0	0	0	0	4	1	1	F	h	1l,g
	Diplostyla concolor (WIDER, 1834)		0	0	0	1	1	0	0	0	0	0	0	2	1	1	G	h	1l,g-2

Dismodicus elevatus (C.L. KOCH, 1838)		0	2	1	1	4	1	2	1	4	0	2	18	1	1	F	x	2
Drapetisca socialis (SUNDEVALL, 1832)		0	0	0	2	1	0	0	0	1	0	0	4	2	1	F	h	1–2
Entelecara congenera (O.P.-CAMBRIDGE, 1879)		0	1	0	0	0	0	0	0	2	0	0	3	1	1	F	h	1g-2
Erigone atra (BLACKWALL, 1841)		0	0	0	0	0	0	0	0	0	2	0	2	1	1	O	eu	1g
Erigone dentipalpis (WIDER, 1834)		0	0	0	0	0	0	0	0	0	4	0	4	1	1	O	eu	1g
***Gongylidiellum latebricola* (O.P.-CAMBRIDGE, 1871)**	*Gonglate*	21	32	4	26	43	12	9	9	14	0	0	170	1	1	G	mid	1l,g,m
Lepthyphantes minutus (BLACKWALL, 1833)		0	0	0	1	1	0	0	1	0	0	0	3	2	1	F	eu	1–2
Lepthyphantes zimmermanni (BERTKAU, 1890)		0	0	0	0	1	0	0	0	0	0	0	1	1	1	F	h	1l
Linyphia hortensis (SUNDEVALL, 1830)		0	0	0	1	0	0	0	1	0	0	0	2	2	1	F	h	1l,g-2
Linyphia triangularis (CLERCK, 1757)		0	0	1	0	0	0	0	0	0	0	0	1	3	1	G	x	1l,g-2
Linyphiidae sp.		63	85	67	74	121	80	93	24	44	11	14	676	–	–	–	–	–
Macrargus rufus (WIDER, 1834)		2	1	7	3	7	2	2	2	2	0	0	28	2	1	F	x	1l,g,m-2
Meioneta affinis (KULCZYNSKI, 1898)		0	0	0	0	0	0	0	0	0	1	0	1	1	1	O	x	1u,g-2

Table A1. Continued.

Family	Species	Abbr.	1999			2000				2001				∑	SC	Web	HAB	MD	STR
			C	F	CC	C	F	CCB	CCS	C	F	CCB	CCS						
	Meioneta rurestris (C.L. KOCH, 1836)		0	0	0	0	0	3	6	0	0	3	9	21	1	1	O	x	1l,g,m,u
	***Micrargus herbigradus* (BLACKWALL, 1854)**	*Micrherb*	8	7	9	14	11	7	7	7	10	0	1	81	1	1	F	mid	1l,g,m
	Minyriolus pusillus (WIDER, 1834)		0	2	1	0	1	0	0	0	0	0	0	4	1	1	F	x	1l
	Moebelia penicillata (WESTRING, 1851)		1	0	0	0	6	1	0	0	0	0	0	8	na	1	F	x	2
	Monocephalus fuscipes (BLACKWALL, 1836)		0	0	0	1	0	0	0	0	0	0	0	1	1	1	F	h	1l
	Neriene peltata (WIDER, 1834)		0	0	0	0	0	0	2	0	0	0	0	2	2	1	F	x	2
	f*Neriene radiata* (WALCKENAER, 1842)		0	0	0	0	0	1	0	0	0	0	0	1	3	1	G	x	1l,g-2
	Obscuriphantes obscurus (BLACKWALL, 1841)		0	1	0	0	0	0	0	0	0	0	0	1	1	1	F	h	1l-2
	Oedothorax apicatus (BLACKWALL, 1850)		0	0	0	0	0	5	0	0	0	11	2	18	1	1	O	eu	1u,g
	Panamomops affinis (MILLER & KRATOCHVIL, 1939)		5	0	0	6	0	0	1	1	0	0	0	13	1	1	G	x	na
	Pelecopsis elongata (WIDER, 1834)		5	1	1	2	3	0	2	1	1	0	0	16	1	1	F	h	1

Pocadicnemis pumila (BLACKWALL, 1841)		0	0	1	0	0	0	7	0	0	0	0	8	1	1	O	eu	1l,g,m
Porrhomma campbelli (O.P.-CAMBRIDGE, 1894)		1	0	0	0	1	0	0	0	0	0	0	2	1	1	F	x	0-1l
Porrhomma montanum (JACKSON, 1913)		0	0	0	0	0	1	0	0	0	0	0	1	1	1	F	h	1l
***Tapinocyba pallens* (O.P.-CAMBRIDGE, 1872)**	Tapipall	220	146	147	21	7	23	17	23	7	4	0	615	1	1	F	h	1l,m
Tapinocyba praecox (O.P.-CAMBRIDGE, 1873)		0	0	0	0	0	1	2	0	0	0	0	3	1	1	O	x	1u,g
Tapinopa longidens (WIDER, 1834)		0	2	1	0	1	0	1	0	1	0	0	6	2	1	F	x	1l,g-2
Tenuiphantes alacris (BLACKWALL, 1853)		1	0	1	0	3	0	0	7	6	0	0	18	2	1	F	h	1l
***Tenuiphantes flavipes* (BLACKWALL, 1854)**	*Tenuflav*	6	17	35	20	18	4	0	19	7	2	8	136	1	1	F	x	1l,g,m-2
Tenuiphantes mengei (KULCZYNSKI, 1887)		0	0	0	0	0	0	0	0	0	1	0	1	1	1	G	h	1l,g,m
***Tenuiphantes tenebricola* (WIDER, 1834)**	*Tenutene*	16	45	17	28	50	0	0	11	16	0	0	183	1	1	F	h	1l
Tenuiphantes tenuis (BLACKWALL, 1852)		0	1	0	0	0	1	1	0	0	0	1	4	1	1	O	x	1l,g,m,u
Troxochrus nasutus (SCHENKEL, 1925)		2	1	0	1	0	0	0	0	1	0	2	7	1	1	F	h	1l,m-2

Table A1. Continued.

Family	Species	Abbr.	1999			2000				2001				∑	SC	Web	HAB	MD	STR
			C	F	CC	C	F	CCB	CCS	C	F	CCB	CCS						
	Walckenaeria alticeps (DENIS, 1952)	*Walcalti*	23	4	10	6	1	4	1	7	3	0	0	59	1	1	G	h	1g,m
	***Walckenaeria atrotibialis* (O.P.-CAMBRIDGE, 1878)**	*Walcatro*	15	21	27	7	8	7	7	18	17	1	2	130	1	1	G	h	1l,g,m-2
	Walckenaeria cucullata (C.L. KOCH, 1836)		9	2	6	6	4	1	0	1	0	0	0	29	1	1	F	x	1l-4
	***Walckenaeria dysderoides* (WIDER, 1834)**	*Walcdysd*	9	5	27	11	0	16	26	4	1	2	0	101	1	1	F	x	1l-2
	Walckenaeria obtusa (BLACKWALL, 1836)		2	0	0	2	0	0	0	0	0	0	0	4	2	1	F	x	1l
Lycosidae (Lyc)	*Alopecosa pulverulenta* (CLERCK, 1757)		0	0	0	0	0	0	0	0	0	0	3	3	3	0	O	eu	1g
	Alopecosa sp.		0	0	2	0	0	11	0	0	1	2	1	17	–	–	–	–	–
	Alopecosa taeniata (C.L. KOCH, 1835)		0	0	1	0	0	5	1	0	0	2	4	13	na	0	G	na	1
	Lycosidae sp.		0	0	0	10	0	571	8	1	1	97	42	730	–	–	–	–	–
	Pardosa agrestis (WESTRING, 1861)		0	0	0	0	0	2	0	0	0	0	0	2	1	0	O	x	1g,u
	Pardosa amentata (CLERCK, 1757)		0	0	0	0	0	0	0	0	0	11	4	15	3	0	O	eu	1g-2
	Pardosa lugubris (WALCKENAER, 1802)	*Pardlugu*	0	0	0	0	0	9	15	0	1	15	2	42	2	0	G	h	1l,g,m
	***Pardosa prativaga* (L. KOCH, 1870)**	*Pardprat*	0	0	0	0	0	51	15	0	0	6	1	73	2	0	O	eu	1g

	Pardosa pullata (CLERCK, 1757)		0	0	0	0	0	1	0	0	0	0	0	1	2	0	O	eu	1g,m
	Pardosa riparia (C.L. Koch, 1833)		0	0	0	0	0	3	1	0	0	0	1	5	1	0	G	h	1–2
	Pardosa sp.		0	0	0	0	0	0	0	0	0	4	2	6	–	–	–	–	–
	Trochosa sp.		0	0	2	0	0	44	2	1	0	41	6	96	–	–	–	–	–
	Trochosa terricola (THORELL, 1856)	*Trocterr*	0	1	18	1	0	19	5	0	4	12	7	67	3	0	G	x	1l,g
	Xerolycosa nemoralis (WESTRING, 1861)	*Xeronemo*	0	0	0	0	0	4	3	0	0	23	15	45	3	0	G	x	1l
Philodromidae (Phi)	Philodromidae sp.		0	0	0	0	0	0	0	0	0	6	0	6	–	–	–	–	–
	Philodromus collinus (C.L. KOCH, 1835)		0	0	1	0	0	0	0	2	1	0	0	4	3	0	F	x	1–2
	Philodromus sp.		0	2	1	4	5	3	4	1	0	0	2	22	–	–	–	–	–
Salticidae (Sal)	*Dendryphantes rudis* (SUNDEVALL, 1832)		0	1	0	0	1	0	0	0	0	0	0	2	2	0	F	x	2
	Euophrys frontalis (WALCKENAER, 1802)		0	0	0	0	0	1	0	0	0	0	0	1	2	1	G	x	1l,g,m,u-2
	Evarcha arcuata (CLERCK, 1757)		0	0	0	0	0	0	1	0	0	0	0	1	3	0	O	eu	1g-2
	Evarcha falcata (CLERCK, 1757)		0	0	0	0	0	0	1	0	0	0	0	1	3	0	O	x	1g-2
	Heliophanus cupreus (WALCKENAER, 1802)		0	0	0	0	0	1	0	0	0	0	0	1	2	0	G	x	2
	Neon reticulatus (BLACKWALL, 1853)	*Neonreti*	1	10	13	3	2	0	2	2	1	7	2	43	1	0	G	h	1l,g,m-2
	Salticidae sp.		1	1	0	4	0	0	2	0	0	1	0	9	–	–	–	–	–

Table A1. Continued.

Family	Species	Abbr.	1999			2000				2001				∑	SC	Web	HAB	MD	STR
			C	F	CC	C	F	CCB	CCS	C	F	CCB	CCS						
	Salticus zebraneus (C.L. KOCH, 1837)		0	0	0	0	0	0	0	0	1	0	0	1	2	0	F	x	2
	Synageles venator (LUCAS, 1836)		0	0	0	0	0	2	0	0	0	0	0	2	2	0	O	eu	1g
Segestriidae (Seg)	*Segestria senoculata* (LINNAEUS, 1758)		0	0	2	1	1	3	0	4	5	0	0	16	3	1	F	x	2
Tetragnathidae (Tet)	*Metellina segmentata* (CLERCK, 1757) synonym: *Meta segmentata*		0	0	0	0	0	0	0	0	0	4	0	4	3	1	G	h	1l
	Metellina sp.		0	0	0	0	1	0	0	0	1	0	2	4	–	–	–	–	–
	Pachygnatha degeeri (SUNDEVALL, 1830)		0	0	0	0	0	0	0	0	0	2	0	2	2	0	O	eu	1g,m,u
	Tetragnatha pinicola (L. KOCH, 1870)		2	2	1	0	2	1	0	0	0	0	0	8	2	1	O	x	2
	Tetragnatha sp.		0	0	0	0	0	0	0	2	0	0	0	2	–	–	–	–	–
Theridiidae (The)	*Achaearanea lunata* (CLERCK, 1757)		0	0	0	0	0	0	3	0	0	0	0	3	2	1	F	h	2
	Robertus lividus (BLACKWALL, 1836)		4	3	3	1	0	0	1	3	1	0	1	17	2	1	F	eu	1l-2
	Theridiidae sp.		7	2	4	7	3	3	7	4	1	2	3	43	–	–	–	–	–
	Theridion bimaculatum (LINNAEUS, 1767)		0	0	0	3	0	5	0	1	0	0	0	9	1	1	G	x	2
	Theridion boesenbergi (STRAND, 1904)		0	0	0	0	0	0	0	0	1	0	0	1	1	1	n.a.	n.a.	1l

	Theridion tinctum (WALCKENAER, 1802)	0	0	0	1	0	0	0	1	0	2	0	4	1	1	F	x	2
Thomisidae (Tho)	*Diaea dorsata* (FABRICIUS, 1777)	0	0	1	1	0	0	0	0	0	0	0	2	2	0	F	mid	2
	Ozyptila trux (BLACKWALL, 1846)	0	0	0	1	0	0	0	0	0	0	0	1	2	0	G	h	1l,g
	Thomisidae sp.	0	0	0	0	0	1	0	0	0	0	0	1	–	–	–	–	–
	Xysticus audax (SCHRANK, 1803)	4	0	3	0	1	1	4	3	1	5	0	22	3	0	G	x	1-4
	Xysticus cristatus (CLERCK, 1857)	1	0	1	0	0	0	1	0	0	1	0	4	3	0	O	x	1g,u-2
	Xysticus kochi (THORELL, 1872)	0	0	0	0	0	0	0	0	0	19	5	24	3	0	O	x	1g,u-2
	Xysticus lanio (C.L. KOCH, 1835)	0	0	0	0	0	1	0	0	0	0	0	1	3	0	F	h	3-4
	Xysticus sp.	4	7	10	4	12	1	6	5	8	4	0	61	–	–	–	–	–
Not classified Individuals		nd	nd	nd	2	8	29	8	8	17	7	4	83	–	–	–		–
All Individuals		859	958	908	623	741	1120	592	376	339	344	241	7101					

Treatment: C = control; F = femel; CC = clear-cut; CCB = clear-cut beech; CCS = clear-cut spruce. nd = not determined. Size classes of females: 1 = 0–3.0 mm, 2 = > 3.0–6.0 mm, 3 = > 6.0–10.5 mm, 4 = > 10.5 mm; web classes: 1 = with web, 0 = no web; habitat categories: F = forested habitats, O = open habitats, G = generalist; humidity categories: h = hygrophilic (in wet and humid habitats), mid = in mid humid / mid dry habitats, eu = euryoecious (independent of humidity), x = xerobiont/-phil (in dry habitats); stratum categories: 0 = underground living (below stones, caves, etc.), 1 = epigeic living (ground-dwellers), 1 g = in grass mulches, 1l = in forest litter, 1 m = in moss, 1u = on uncovered places, 2 = aboveground places (bushes trees etc.) Species printed in bold comprised more than 1% of individuals of the total sample.

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