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The arthropod community of boreal Norway spruce forests responds variably to stump harvesting

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Abstract

Forest fuel harvesting increases the need to collect not just logging residues but also tree stumps from harvested stands. This biomass removal has raised concern over forest biodiversity. Here, the effects of stump harvesting on spiders, ants, harvestmen, ground beetles and epiedaphic springtails occupying boreal Norway spruce (*Picea abies*) forest floor were studied two and five years after harvesting by comparing pitfall trap samples from clear-cut sites with and without subsequent stump harvesting and from unharvested mature forests in central Finland. At harvested sites, traps were placed both on intact and exposed mineral soil surface. Open-habitat and generalist ground beetles benefitted from the stump harvesting, but generally the numbers of arthropods between stump harvesting treatments and different aged clear-cuts were rather similar. The intact forest floor hosted more ants, springtails and harvestmen than did the exposed mineral soil. Moreover, the community structure of spiders, ground beetles and springtails was affected by stump harvesting, forest-floor quality (intact or exposed), and time elapsed since harvesting. Based on these results we recommend minimizing the exposure of mineral soil during management practices. However, more long-term studies are required to document the development of fauna in the harvested areas and the ecosystem-level impacts of utilization of forest biomass for energy.

Key words: Araneae; Bioenergy; Carabidae; Collembola; Formicidae; Opiliones

1. Introduction

Since the beginning of 2000s, the harvesting of logging residues, stems and stumps has considerably intensified the Fennoscandian forestry (Koistinen and Äijälä, 2005; Rudolphi and Gustafsson, 2005). In particular, stump harvesting has increased (Saarinen, 2006; Ylitalo, 2013). Until recently, stumps were removed from forests only if infected by the root rot (*Heterobasidion* or *Armillaria* spp.) (Halonen, 2004; Thies and Westlind, 2005; Zabowski et al., 2008). Stump harvesting may have many impacts on biota similar to top-soil preparation and removal of logging residues after harvesting. It improves site for tree saplings, but simultaneously the procedure removes much organic matter and carbon from forests, increases soil erosion and compaction, impoverishes soil nutrient stocks and cycling, and removes key structures and resources from a myriad of forest organisms (Walmsley and Godbold, 2010). Many impacts of stump harvesting are considerably more severe than mounding or harrowing of harvested sites, as many structural elements, such as dead wood, forest floor and soil physical characteristics, are altered through stump removal (Siitonen, 2008; Rabinowisch-Jokinen and Vanha-Majamaa, 2010; Kataja-aho et al., 2011a).

The intermediate disturbance hypothesis postulates that species richness will be highest in areas with intermediate levels of disturbance (Connell, 1978). Such general pattern might result from different responses of species associated with undisturbed and highly disturbed habitats. Indeed, open-habitat associated ground beetles (carabids;Coleoptera, Carabidae) benefit from clear cutting, whereas closed-forest associated species decrease, but do not necessarily disappear (e.g., Koivula, 2002; Koivula, 2012). However, compared to clear cutting followed by modest top-soil preparation, stump harvesting is a considerably more intensive disturbance at least for organisms living in the forest floor. During stump harvesting with excavators, ca. 70% or occasionally up to 90% of the soil surface is exposed to mineral soil due to stump lifting and machinery movements, whereas less than 40% is exposed at the clear-cut sites with traditional site preparation (mounding) (Kataja-aho et al., 2011a, 2011b). Thus, stump harvesting may not represent an “intermediate disturbance” but rather “an intensive disturbance" for many invertebrate taxa living in forest floor and concomitantly drastically alter forest biodiversity.

Local invertebrate species richness may increase after clear cutting as forest generalists persist and many open-habitat species colonize the sites (Niemelä, 1997). Forest habitats change remarkably during clear cutting, which may be reflected e.g. in species richness of hunting and web-building spiders (Araneae) that are dependent on particular structural elements of forest (Larrivée et al., 2005) and carabid beetles that respond to logging and within-site variation according to their associations with tree-canopy closure and soil moisture (Niemelä et al., 1988; Niemelä and Halme, 1992). In addition, mounds of *Formica* wood ants are generally smaller and host fewer individuals in clear-cuts than in standing forests (Sorvari and Hakkarainen, 2005). This may have consequences on forest ecosystem functioning since ants, particularly red wood ants (*Formica rufa* group), are considered keystone species of European and Asian boreal and mountain forests because of their contribution to ecosystem carbon and nutrient pools and fluxes (e.g., Rosengren et al., 1979; Laine and Niemelä, 1980; Risch et al., 2005; Finér et al., 2013).

Nittérus et al. (2007) found that the removal of logging residues from clear-cuts results in an increase of generalist carabid beetles and a decline in carabids associated with closed tree canopy 5−7 years after the operations compared to sites where slash is left on the ground. Hence, large-scale biofuel harvesting might cause a shift in species dominance and changes in community composition of forest-floor arthropods. On the other hand, many euedaphic decomposers are well buffered against the initial impacts caused by clear cutting and site preparation and, although microbial biomass may decrease in regenerated areas, changes may not necessarily occur at higher trophic levels of food webs (Siira-Pietikäinen et al., 2001; Siira-Pietikäinen et al., 2002).

Spiders, ants and carabid beetles are important predators in boreal forest floor (Roberts, 1985; Hölldobler and Wilson, 1990). They feed on detritivores, herbivores and other carnivores, thus being top predators of forest-floor food webs (Roberts, 1996; Townsend et al., 2004; Miyashita and Niwa, 2006). Spiders and ants also act as a link between the below- and above-ground biota as they feed on fauna from both sources (Hölldobler and Wilson, 1990; Miyashita et al., 2003). The present study focuses on spiders, harvestmen, ants and carabid beetles because as top predators they are particularly prone to disturbances. Spiders and carabids also rapidly respond to changes in their habitat (Pearce and Venier, 2006; Koivula, 2011, 2012) and are easy to sample in sufficient numbers for statistical analyses (Nilsson et al., 2001). In addition, epiedaphic springtails (large collembolans) are an abundant prey in forest floor food webs (Siira-Pietikäinen et al., 2002).

The aim of the present study was to examine the difference in numbers, species richness and community structure of ground-dwelling arthropods (spiders, harvestmen, ants, collembolans and carabid beetles) in clear-cuts with stump harvesting, clear-cuts with stump retention, and mature unharvested forests. Data in the present study consist of pitfall trap catches that reflect species-specific "activity densities" rather than true relative abundances (e.g. Greenslade, 1964). These catches are hereinafter referred to as "abundance" (unless specified otherwise) for convenience. The following questions are examined using data collected at replicated sites harvested in different times:

i) Are there differences in abundance and community structure of ground-dwelling arthropods between stump harvesting and stump retention sites?

ii) Does the quality of forest-floor habitat in clear-cuts (here, exposed mineral soil or intact forest floor) affect these taxa?

iii) Are there differences in abundance or community structure of ground-dwelling arthropods in clear-cuts at different successional stages?

2. Materials and methods

2.1 Study sites and experimental design

The study was carried out in central Finland (61°48´N, 24°47´E) in boreal Norway spruce (*Picea abies* (L.) Karst.) dominated forest stands (sites) growing on Myrtillus (MT) or Oxalis-Myrtillus (OMT) site types (Cajander, 1926). The field layer of MT forest is characteristically dominated by *Vaccinium myrtillus*, *V. vitis-idaea* and *Linnaea borealis*, whereas that of OMT forest is dominated by *V. myrtillus, L. borealis, Oxalis acetosella, Maianthemum bifolium* and *Convallaria majalis* (Hotanen et al., 2008). The soil in the study area was podzolised moraine with a 3-4 cm thick organic layer; mean annual temperature was 4.9°C and annual precipitation was 646 mm in 2007. The ground was completely snow covered for approximately three months during the winter 2007 (Finnish Meteorological Institute, 2008).

Twenty-five study sites were selected for our study. The same sites had previously been used to study decomposer communities (Kataja-aho et al., 2011a). At the time of the present study, ten of these sites had been clear-cut five years before (“5 years old sites”), and ten sites had been clear-cut two years before (“2 years old sites”) the present study. Following clear cutting, ca. 70% of the logging residues had been removed from all sites, and stumps had been removed from half of them (five in both harvesting years) using an excavator equipped with a stump-removal bucket. Soil had been prepared by mounding at all sites with an excavator by inverting a scoop of soil on top of the ground nearby. The study design involved five replicates of each combination of stump treatment (harvested or retained) and age (harvesting done 2 or 5 years earlier). All harvested sites had subsequently been planted with nursery-produced 1.5 years old Norway spruce seedlings. All the management and regeneration practices had been done according to the prevailing guidelines for Finnish forestry (Metsätalouden kehittämiskeskus Tapio, 2006). The area of clear-cut sites varied between 0.5 and 4.5 hectares. In addition to the clear-cut sites, five unharvested mature Norway spruce sites (hereinafter referred to as “mature forests”) were selected to derive reference data for the effects of clear cutting.

At each site, a ca. 30 m × 30 m (900 m^2) study plot for vegetation and arthropod samplings (see below) was chosen by avoiding moist and rocky patches. The distance from the plot to the nearest stand edge was at least 30 meters to avoid severe edge impact. The proportions of intact soil and the soil exposed to mineral surface were estimated for each plot (Kataja-aho et al., 2011a). Soil surface consisting of mixed mineral and organic soil layers was classified as disturbed mineral soil surface.

2.2 Sampling and sample treatments

Arthropods were collected using pitfall traps made of 2-dl plastic cups set flush with soil surface, and covered with 10 cm × 10 cm plastic sheets placed a few cm above the soil surface to prevent rain and litter from entering the traps. The traps were half-filled with 50% ethylene glycol to kill and preserve arthropods falling into the traps. Eight traps were set at each site; at harvested sites, four traps were placed on surface that had originally been exposed to mineral soil and four on intact soil surface. The traps were placed in two parallel rows ca. 5 m apart (i.e. 2 × 4 traps; Fig. 1). The type of surface for each trap was randomized in a pair-wise manner. At each mature-forest site, all eight traps were placed into intact soil. Altogether 200 pitfall traps per sampling period were used in the study.

Fig. 1.

Data were collected over three 10-days periods in 2007. The first sampling period was from 28th of May to 7th of June ("spring"), the second was from 9th to 19th of July ("summer") and the third was from 10th until 20th of September ("autumn").

Spiders, harvestmen, carabid beetles, ants and collembolans were counted, and groups other than harvestmen were identified to species. Due to labor restrictions, spiders, harvestmen and ants were identified only from six traps per study plot; three from mineral soil surface and three from untreated soil surface. Similarly, six out of eight pitfall traps were taken into account when collecting and analyzing these three groups from the mature forests. All eight traps per site were investigated for carabid beetles and collembolans.

Vegetation surveys were done at each study plot on 10th of July 2007 by identifying plants to species and estimating their percent covers from ten 0.5 m × 0.5 m subplots; five of these were on mineral soil surface and five were on intact soil surface (Kataja-aho et al., 2011a). Here, only the covers of ground- and field-layer vegetation were used as explanatory variables for the abundance and species richness of studied animal groups.

2.3 Statistical analyses

For the statistical analyses the data from all three sampling periods were pooled. The numbers and species richness of arthropods were analyzed using a split-plot ANOVA to evaluate the effects of stump harvesting, time elapsed since harvesting operations (age of the site), and the quality of soil surface (intact soil or exposed mineral soil). The split-plot ANOVA was used because the samples for each surface-quality type within a given site were not independent replicates for stump harvesting or site age. Hence, the surface acted as a within-subjects factor and was plotted with the treatment and the age of the site (the between-subjects factors) in the analyses. Variation in the arthropod community structure was analyzed using non-metric multidimensional scaling (NMDS) with a Bray-Curtis distance matrix and multi-response permutation procedures (MRPP) (Zimmermann, 1985) in PC-ORD 5.33 software. The abundance and species richness of arthropods in the traps of intact soil surface were compared between mature forests and clear-cuts using the age of the site as the only explanatory variable (two or five years since clear cutting, or mature uncut forest). These data were analyzed with a univariate ANOVA, and possible significant effects were evaluated using Tukey's post hoc tests. Mechanistic causes for possible differences between treatments were explored by calculating Spearman rank correlations between vegetation cover and abundance or species-richness of arthropods. The ANOVA and correlation analyses were done using IBM SPSS Statistics software, version 22.

Results

3.1 Effects of stump harvesting on macroarthropods

Altogether more than 42,000 individuals and 170 arthropod species were captured, counted and identified (Table 1). The numbers of captured spiders, ants, harvestmen and collembolans between the stump harvesting and stump retention sites were rather similar (Fig. 2, Table 2). The abundance and species richness of carabid beetles were higher at the stump harvesting sites compared to the stump retention sites (Table 2, Figures 2 and 3). The stump retention sites harbored more spider species than the stump harvesting sites (Table 2, Fig. 3).

Table 1

Fig. 2.

Fig. 3.

3.2. Effects of soil surface quality on macroarthropods

More harvestmen and ants were captured from the intact forest floor than from the exposed mineral soil. In the five year old stands the intact forest floor harbored more spiders than did the exposed mineral soil (Table 2, Fig. 2). At the two year old sites collembolans were more abundant on the intact forest floor than on the exposed mineral soil (Table 2, Fig.2). Ants were more speciose on the intact forest floor compared to the exposed mineral soil (Table 2, Fig. 3). Generally, the covers of ground- and field-layer vegetation only occasionally and inconsistently correlated with the abundance or species richness of the studied invertebrates (Supplementary material, Table 1).

3.3. Effects of stand age on macroarthropods

Age of the clear-cut site had negligible effects on the abundances of the studied animal groups. Mature forests did not significantly differ from the clear-cuts in terms of the abundance of carabid beetles, ants or collembolans (Table 3, Fig. 2). Harvestmen were more abundant in the mature forests compared to the clear-cuts (Table 3, Fig. 2). Spiders were significantly and positively affected by clear-cutting. In addition, the older clear-cuts harbored more spider species than did the younger clear-cuts (Tables 2 and 3, Figures 2 and 3). The species richness of collembolans was higher at the two-years old sites compared to the five-years old sites (Tables 2 and 3, Figures 2 and 3). The species richness of carabids or ants did not differ significantly between the mature forests and the clear-cuts (Table 3, Fig. 3).

Table 2

Table 3

3.4 Community structure of macroarthropods

3.4.1 Spiders

The community structure of spiders differed between the stump harvesting and stump retention sites and between the two- and five-years old clear-cuts and between the soil-surface categories (Table 4, Fig. 4). The lycosid genus *Pardosa* was the most abundant genus of spiders (58% of all spiders), and *P. riparia* and *P. pullata* were the most abundant species in this genus (Supplementary material, table 5). Approx. 97% of the individuals in the genus *Pardosa* were caught from the clear-cuts and less than 3% were sampled in the mature forests during the first sampling period. However, no significant differences were found in the abundance of *P. riparia* or *P. pullata* between the stump treatments or site ages. *Pardosa riparia* was more abundant on the intact forest floor compared to the mineral soil surfaces ($F_{(1,16)} = 13.449$; $p = 0.002$, Supplementary material, table 5). Whereas *P. pullata* was more abundant on the mineral soil surface compared to intact forest floor ($F_{(1,16)} = 14.325$; $p = 0.002$, Supplementary material, table 5). Also the family Gnaphosidae was almost exclusively captured in the clear-cuts (98% of the specimens); the most abundant species was *Gnaphosa bicolor.* One *Pardosa* species, *P. lugubris,* was found also in mature forests (18% of the specimens) and the abundant linyphiid *Tenuiphantes alacris* was caught mainly in mature forests (90% of the specimens). As a whole, the family Linyphiidae was captured both in the mature forests (35% of the specimens) and in clear-cuts (65%).

3.4.2 Ants

The community structure of ants was not analyzed with NMDS because the group largely consisted of just one dominant species group, *Formica rufa*, which accounted for more than 90% of the captured ant individuals (Supplementary material, table 2). The abundance of *F. rufa* did not significantly differ between the stump treatments, site ages or soil-surface quality categories.

3.4.3 Carabid beetles

The community structure of carabids differed between the stump treatments and site-age categories (Table 4, Fig. 4). The five most abundant species were *Pterostichus oblongopunctatus*, *P. versicolor*, *P. niger*, *Cicindela campestris* and *Bembidion lampros*. *Pterostichus oblongopunctatus* and *P. niger* were found at all sites, but they were most abundant in the mature forests (Supplementary material, table 4). *Pterostichus versicolor, B. lampros* and *C. campestris* were not found in the mature forests, and the latter was solely caught in the two-years old clear-cuts and mainly from the mineral soil surface during the spring sampling period.

3.4.4 Collembolans

The community structure of collembolans did not differ significantly between the stump-harvesting treatments but was different between the site-age and soil-surface categories (Table 4, Fig. 4). Three most abundant collembolans over the whole study period were *Orchesella flavescens*, *Lepidocyrtus lignorum* and *Pogonognathellus flavescens* (Supplementary material, table 3). *Orchesella flavescens* was more common in two-years old compared to the five-years old clear-cuts ($F_{(1,16)} = 22.29$; $p < 0.001$) and on the intact forest floor than on the mineral soil surface ($F_{(1,16)} = 25.11$; $p < 0.001$, Supplementary material, table 3). More *L. lignorum* and *P. flavescens* were caught in the five-years old than in the two-years old clear-cuts ($F_{(1,16)} = 7.46$; $p = 0.015$; $F_{(1,16)} = 27.48$; $p < 0.001$, respectively).

Fig. 4.
Table 4.

4. Discussion

Stump harvesting exposes mineral soil on larger areas and mixes the soil layers deeper than commonly used site preparation (Kataja-aho et al., 2011a). Thus, stump harvesting not only removes stumps but also changes the quality and structure of soil surface. Furthermore, stump harvesting changes the decomposer community and enhances the decomposition of organic matter and nitrogen mineralization (Kataja-aho et al., 2012), and it also increases the diversity of plant community during the first few years following the procedure (Saksa, 2013). The present results also showed that the community structure of spiders, carabid beetles and collembolans was affected by stump harvesting, forest floor quality and time elapsed since harvesting. However, stump harvesting affected negatively only the numbers of spider species. The results also indicated that some arthropod groups – most notably ants, collembolans and harvestmen – respond only weakly to stump harvesting but are more abundant in intact forest floor. Hence, the indirect effects of stump harvesting on macroarthropods, due to changes in the quality of soil surface seem to be clear.

However, the most abundant spider species at our study sites were lycosids that actively hunt for prey and are thus likely to benefit from the increased area of bare soil in their habitat (Almquist, 2005). The same holds also for the family Gnaphosidae (Koponen, 2013). The availability of suitable microhabitats in a forest-floor mosaic, and abiotic factors such as solar radiation and soil moisture, are important for many species for example among spiders and ants (Huhta, 1971; Koponen et al., 1975; Niemelä et al., 1996).

The abundance and species richness of carabids were higher at the stump-harvesting than at the stump-retention sites in the present study. Generalist and open-habitat species, such as *P. oblongopunctatus*, *P. niger, C. campestris* and *B. lampros*, benefited from stump harvesting compared to stump retention, although *P. oblongopunctatus* and *P. niger* were most numerous in mature forests. Pihlaja et al. (2006) found that forest carabids in clear-cuts prefer undisturbed patches over bare-soil patches, whereas open-habitat species show the opposite association. Stump-harvesting sites provide more and larger patches of micro-habitats suitable for open-habitat species compared to sites that have only been logged and prepared (Kataja-aho et al., 2011a). Furthermore, open-habitat species prefer relatively warm microhabitats (Thiele, 1977). The daytime temperatures are higher in plots of exposed mineral soil than in plots where the soil is extensively covered by field-layer vegetation and humus (Kubin and Kemppainen, 1994).

We found that epiedaphic collembolans seemed to somewhat suffer from stump harvesting due to changes in soil-surface microhabitat, which corroborates our earlier observations (Kataja-aho et al., 2011b). Collembolans are common prey for spiders (Marra and Edmonds, 1998) and were generally least numerous in spring when the abundance of spiders was high (Table 1). On the other hand, they were abundant in the autumn period when there were hardly any spiders present and their food resources, litter and fungal hyphae, were plentiful (Coleman et al., 2004). Thus, the collembolan community might have been affected by direct predator-prey interactions. However, other

– not mutually exclusive – explanations include possible internal dynamics between adult and juvenile collembolans, and the phenology and overwintering success of species.

Clear cutting severely impacts some forest-floor arthropods, but these organisms also appear to begin to recover within a few years after the disturbance event (e.g., Niemelä et al., 2007, Siira-Pietikäinen and Haimi, 2009). In the present study clear cutting itself affected spiders and harvestmen; spiders benefited from clear-cutting whereas there were clearly more harvestmen in the mature forests than in the clear-cuts. On intact forest floor, the abundance and species richness of spiders were lower in two-years old as compared to five-years old clear-cuts. Abiotic factors, such as light intensity and soil moisture that are affected by the developing vegetation, have large effects on spiders (Huhta, 1971; Koponen, 2005). However, we found no significant and consistent correlation between plant cover and the abundance or species richness of spiders. This finding does not mean that qualitative changes in plant community could not have affected the spider communities through physical and/or chemical factors.

Forests are the main habitat for ca. 38% of threatened species in Finland (Rassi et al., 2010). Changes in the age structure of forests and shortage of dead wood in managed forests are among the most important reasons for 29 spider and 308 coleopteran species for being red-listed (Rassi et al., 2010). In our study, none of the 170 identified species were endangered, but it should be noted that 11 species were only found in mature forests, of which nine were spiders and two were carabids. Correspondingly, 74 spider species and 28 carabid species were only caught from clear-cuts. Species associated with closed-canopy forests, and with primeval forests in particular, respond negatively to clear cutting, while many other species survive in sufficiently large retention-tree groups within clear-cuts (Pajunen et al. 1995; Niemelä, 1997; Matveinen-Huju et al., 2006; Oxbrough et al., 2006). However, invertebrate species that are dependent on stumps for breeding, shelter or foraging are lost from clear-cuts if stumps are removed and no compensatory dead wood is available (Jonsell and Hansson, 2011; Andersson, 2012; Persson et al., 2013). It should be noted that pitfall traps do not sample all arthropod species and species living in the stumps are mainly missed. Moreover, fauna in dead wood was not studied here but they should be taken into account when exploring the overall effects of stump harvesting on forest biodiversity.

5. Conclusions

We showed that, in the short term, (1) clear cutting impacts spiders and harvestmen, but (2) stump removal has minor additional effects on these taxa, and (3) open-habitat and generalist carabids even benefit from stump harvesting. Moreover, (4) changes in microhabitats due to forestry operations affected ants, collembolans and harvestmen, as more individuals or species were found in intact soil surface as compared to the exposed mineral soil. Stump harvesting decreases the amount of intact forest floor, and arthropods show variable responses to such changes in their habitat. Hence, from an arthropod perspective, it may be premature to conclude that stump harvesting would be an intensive disturbance. However, we cautiously recommend to retain as much intact forest floor as possible at harvested sites and to avoid destroying large pieces of dead wood, including old stumps, to secure habitat for organisms that rely on these resources in commercial forests (Persson et al., 2013). When refining the guidelines and methods of stump harvesting, all relevant impacts of the procedure should be a priori carefully considered: the practice affects the fertility of soil (Walmsley and Godbold, 2010; Tamminen et al., 2014), lichens (Hämäläinen et al., 2015), arthropod communities (this paper and e.g., Jonsell and Hansson, 2011) and soil decomposers (Kataja-aho et al., 2011a). Large-scale stump harvesting is a relatively new procedure, and the time scale in the present study was probably too short to demonstrate long-term impacts of stump harvesting. Thus, longer-term studies are needed to fully understand ecosystem-level impacts of forest-based bioenergy production, including possible extinction debt.

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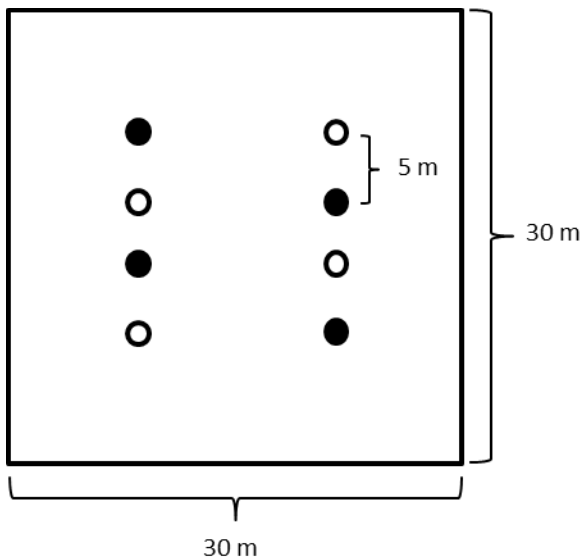

Figure 1. A diagram (out of scale) of the experimental setup of each clear-cut study site, showing the distance between pitfall traps and how the pitfall traps were placed in two parallel rows. Black circles represent traps on exposed mineral soil and white circles traps on intact forest floor. In the mature forest the setup was the same but all the eight traps were placed on intact forest floor.

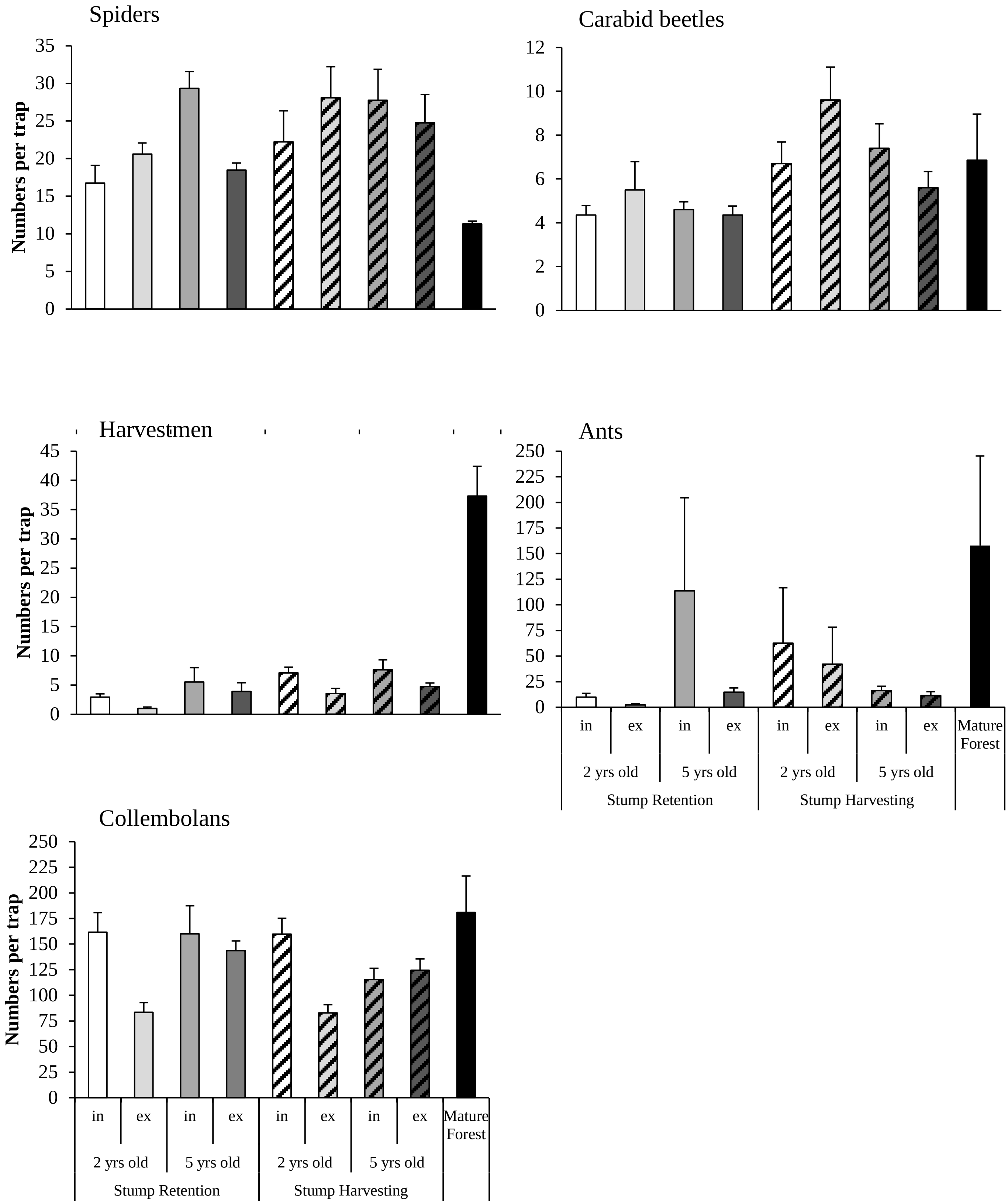
Spiders
Carabid beetles
Harvestmen
Ants
Collembolans
Numbers per trap
in
ex
2 yrs old
5 yrs old
Stump Retention
Stump Harvesting
Mature Forest

Figure 2. Mean numbers (±S.E.) of spiders, carabid beetles, harvestmen, ants and collembolans per trap for different site types. Cross-hatched bars refer to stump harvesting; clear bars (except black) to stump retention; black bars to mature forest; in = intact forest floor; ex = exposed mineral soil.

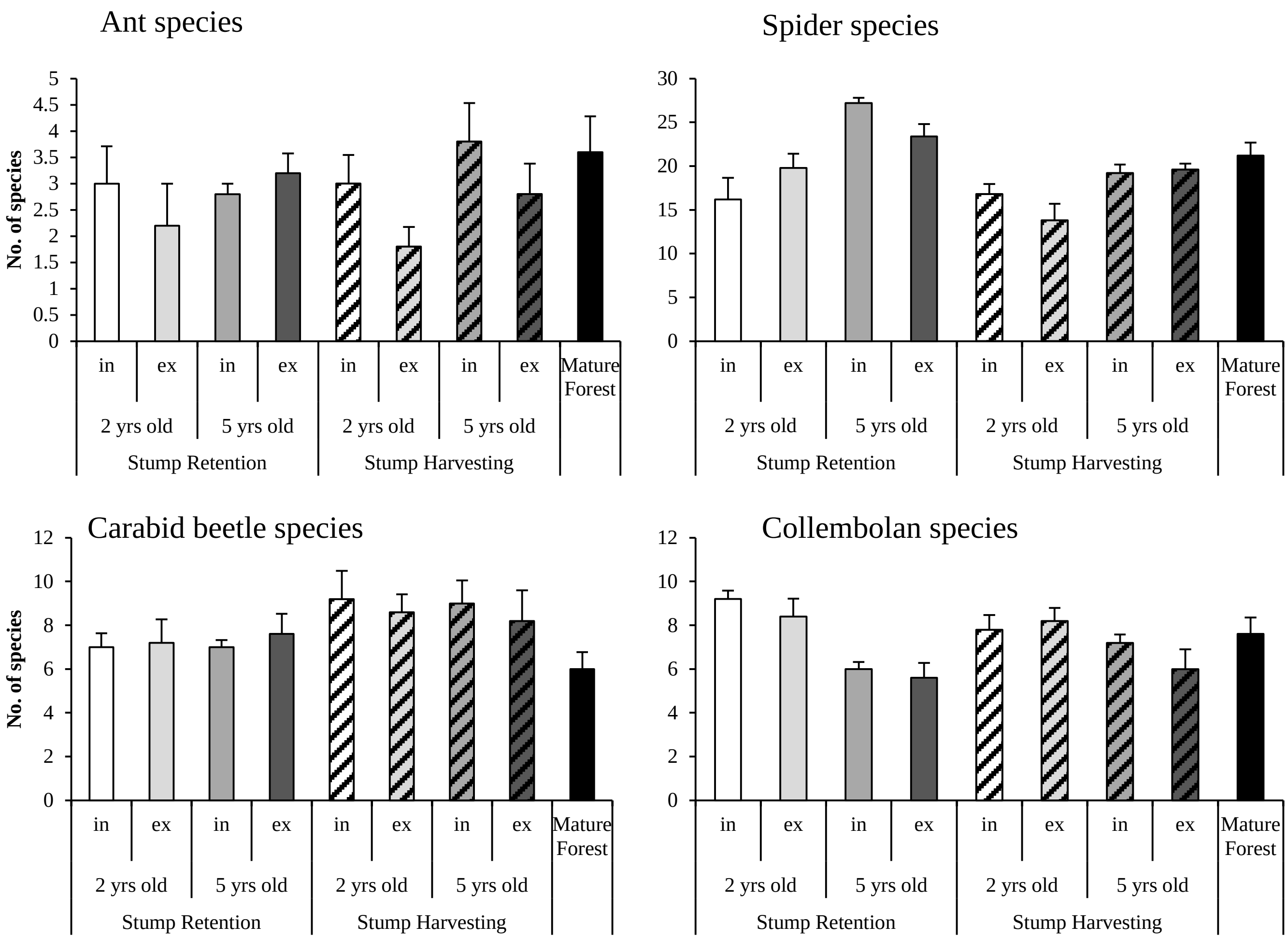

Figure 3. Mean species richness i.e. number of species (±S.E.) of ants, spiders, carabid beetles and collembolans for different site types. Cross-hatched bars refer to stump harvesting; clear bars (except black) to stump retention; black bars to mature forest; in = intact forest floor; ex = exposed mineral soil.

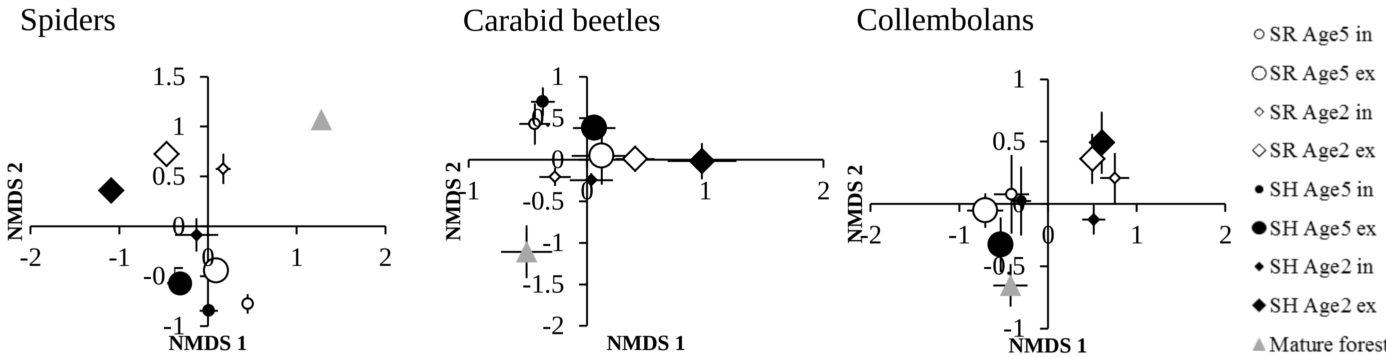

Figure 4. Non-metric multidimensional scaling for the assemblage structure of spiders, carabid beetles and collembolans among the study sites (n = 5 for each site category). In the legend: SH = stump harvesting, SR = stump retention, ex = exposed mineral soil, in = intact soil surface.

Table 1. Total numbers of captured invertebrates and species during each sampling period in the present study.

Species group	Spring	Summer	Autumn	Total	No. of species
Spiders	2731	340	84	3155	113
Ants	3829	4056	438	8323	12
Harvestmen	163	284	1218	1665	Not identified
Carabid beetles	781	357	98	1236	36
Collembolans	4684	10224	12895	27803	9
Total	12188	15261	14733	42182	170

Table 2. Test statistics from the split-plot ANOVA for the effects of soil-surface quality, stump harvesting and site age on the abundance and species number of the arthropod groups. Surface: in = intact forest floor, ex = exposed mineral soil. Harvesting: SH = stump harvesting, SR = stump retention. Age: 2 = two years old clear cut, 5 = five years old clear cut.

			Abundance			Number of species (SPP)		
Group	Treatment	df	*F*	*p*	Difference	*F*	*p*	Difference
Carabids	Surface	1,16	0.665	0.427		0.042	0.840	
	Surface * Age	1,16	6.185	0.024		0.005	0.946	
	Surface * Harvesting	1,16	0.007	0.936		0.569	0.461	
	Surface * Age * Harvesting	1,16	1.810	0.197		0.042	0.840	
	Age	1,16	1.481	0.241		0.006	0.941	
	Harvesting	1,16	9.258	0.008	SH > SR	5.354	0.034	SH > SR
	Age * Harvesting	1,16	0.484	0.497		0.139	0.714	
Spiders	Surface	1,16	0.623	0.441		0.875	0.363	
	Surface * Age	1,16	20.31	<0.001		1.786	0.200	
	Surface * Harvesting	1,16	3.550	0.078		0.643	0.434	
	Surface * Age * Harvesting	1,16	1.255	0.279		13.02	0.002	
	Age	1,16	0.935	0.348		20.18	<0.001	5 > 2
	Harvesting	1,16	1.806	0.198		11.48	0.004	SR > SH
	Age * Harvesting	1,16	0.398	0.537		1.590	0.225	
Ants	Surface	1,16	12.39	0.003	in > ex	8.048	0.012	in > ex
	Surface * Age	1,16	0.323	0.578		2.333	0.146	
	Surface * Harvesting	1,16	2.376	0.143		3.857	0.067	
	Surface * Age * Harvesting	1,16	1.461	0.244		1.190	0.291	
	Age	1,16	2.853	0.111		1.523	0.235	
	Harvesting	1,16	0.027	0.872		0.009	0.926	
	Age * Harvesting	1,16	0.546	0.471		0.225	0.641	
Harvestmen	Surface	1,16	11.61	0.004	in > ex	Not measured		
	Surface * Age	1,16	0.118	0.736				
	Surface * Harvesting	1,16	0.967	0.340				
	Surface * Age * Harvesting	1,16	0.013	0.910				
	Age	1,16	2.033	0.173				
	Harvesting	1,16	3.499	0.080				
	Age * Harvesting	1,16	0.556	0.467				
Collembolans	Surface	1,16	14.96	0.001	in > ex	1.481	0.241	
	Surface * Age	1,16	12.41	0.003		0.533	0.476	
	Surface * Harvesting	1,16	0.407	0.533		0.059	0.811	
	Surface * Age * Harvesting	1,16	0.332	0.573		1.481	0.241	
	Age	1,16	1.086	0.313		22.38	<0.001	2 > 5
	Harvesting	1,16	1.541	0.232		0.000	1.000	
	Age * Harvesting	1,16	1.301	0.271		2.960	0.105	

Table 3. Test statistics from the univariate ANOVA for the differences between clear-cut sites (two- and five-years old) and mature forest; only samples from intact soil surface were considered. Abundance (TOTAL) and species richness (SPP) of different groups of macroarthropods. For significant differences, pair-wise comparisons were made using Tukey's post hoc test (*I-J* value). M = mature forest; 2 = two years old clear-cut, 5 = five years old clear-cut.

	Tukey's comparisons	df	*F*	*I-J*	*p*	Difference
Carabids TOTAL		2,22	0.06		0.940	
Carabids SPP		2,22	1.86		0.177	
Spiders TOTAL		2,22	14.04		<0.001	
	M - 5	2,22		-0.85	<0.001	5 > M
	M - 2	2,22		-0.44	0.035	2 > M
	5 - 2	2,22		0.41	0.015	5 > 2
Spiders SPP		2,22	6.73		0.005	
	M - 5	2,22		-2.00	0.658	
	M - 2	2,22		4.70	0.120	
	5 - 2	2,22		6.70	0.004	5 > 2
Ants TOTAL		2,22	1.32		0.287	
Ants SPP		2,22	0.35		0.707	
Harvestmen TOTAL		2,22	21.29		<0.001	
	M - 5	2,22		1.78	<0.001	M > 5
	M - 2	2,22		1.93	<0.001	M > 2
	5 - 2	2,22		-0.15	0.825	
Collembolans TOTAL		2,22	1.11		0.347	
Collembolans SPP		2,22	5.50		0.012	
	M - 5	2,22		1.00	0.346	
	M - 2	2,22		-0.90	0.419	
	5 - 2	2,22		1.90	0.008	2 > 5

Table 4. Multi-response permutation procedures (MRPP) for the effects of stump harvesting, age of the site and soil-surface type on the species composition of spiders, carabid beetles and collembolans. The test statistic (*T*), chance-corrected within-group agreement (*A*) and statistical significance (*p*) are presented. A summary of non-metric multidimensional scaling (NMDS) for the assemblage structure of spiders, carabids and collembolans among the study sites (n = 5 for each site type).

	Spiders			Carabids			Collembolans		
MRPP	*T*	*A*	*p*	*T*	*A*	*p*	*T*	*A*	*p*
Stump harvesting	-10.93	0.15	<0.001	-4.50	0.037	<0.001	-1.49	0.023	0.083
Age	-17.64	0.25	<0.001	-7.12	0.058	<0.001	-10.13	0.157	<0.001
Soil-surface type	-5.21	0.05	<0.001	-1.18	0.007	0.123	-4.71	0.049	0.002

NMDS	Spiders	Carabids	Collembolans
Final stress	15.8	23.5	7.2
Solution	2-dimensional	2-dimensional	3-dimensional
Final instability	0.0021	0.0029	0.0000
No. of iterations	200	200	200
Plot of stress vs. iteration number	46.93	67.21	38.71