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Effects of stump removal on soil decomposer communities in undisturbed patches of the forest floor

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Running headline: Effects of stump removal on decomposers

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Abstract: Soil preparation after clear cutting leads to fragmentation of forest floor and, consequently, changes the habitat of decomposers. Stump removal for bioenergy is further increasing the disturbance in the soil. We studied responses of decomposers to stump removal in boreal spruce forests during the first four years after clear felling in relation to mounding. Samples for each decomposer organism group were taken from undisturbed forest floor patches which are the main habitat for decomposers after forest regeneration and whose amount and size obviously differ between the treatments. Microbial biomasses and community structure, and the abundance of enchytraeids were not found to be affected by the stump removal. The abundance of nematodes and the total numbers of collembolans were lower in the stump harvesting plots compared to the mounded plots three years after the regeneration. In addition, microbivorous macroarthropods had higher abundances in the mounded plots. Together, decomposer community in the fragments of undisturbed forest floor only slightly differed between the mounded and stump removal areas. However, more data are urgently needed to find out also the longer term effects of stump removal on the forest soil decomposers and their functioning and the development of decomposer community in exposed mineral soil.

Keywords: Forest management, forest soil, fragmentation, nutrient cycling, soil fauna, stump harvesting

Introduction

At present, human-caused habitat loss and fragmentation are the main threats for many organisms. However, fragmentation may not be seen only as a negative consequence of human activities. According to the metapopulation theory (Hanski 1999) habitat fragments that remain undisturbed or are only slightly changed may later act as sources for colonization of damaged patches thus preventing population extinctions at landscape level. In boreal forests, various forest management practices change the forest floor by removing the vegetation and organic soil layers, thereby exposing the mineral soil. Large amount of organic matter is also mixed with mineral soil. As a consequence, the habitat of soil organisms changes: the continuous forest floor fragments into mosaic of patches of different habitat quality.

In general, soil organisms seem to be rather resistant to habitat fragmentation (Rantalainen et al. 2008). The habitat scale of decomposers is usually smaller than that of aboveground fauna depending, however, on the body sizes, mobility and territory sizes of the organisms. As forest soil is usually heterogeneous, even a small area can provide suitable habitats and resources for numerous organisms. For example, a square meter of boreal forest soil can be inhabited on average by 2.4 millions of nematodes, 50 000 enchytraeid worms and 80 000 collembolans (Huhta et al. 1986), and ca. 94 000 km fungal hyphae (calculated from Persson et al. 1980) and 10-15 x 10^{13} cells of bacteria (Persson et al. 1980). Thus, it is important to bear in mind that habitat sizes and diversity patterns differ significantly between above- and belowground communities, the diversity appearing to be very context dependent (De Deyn and Van der Putten 2005).

Species richness is probably not the driving force in soil decomposition processes since it has been shown that some key-stone organism groups, such as mycorrhizal fungi (Allen 1991) or even a single species, such as an enchytraeid worm *Cognettia sphagnetorum*, are able to control the decomposition processes (Huhta et al. 1998; Laakso and Setälä 1999). However, because the aboveground and belowground components of ecosystems are closely interlinked, habitat fragmentation may affect soil organisms indirectly, through changes in the populations of aboveground organisms (particularly plants). In turn, feedbacks from the decomposer community may modify the performance of aboveground organisms (Wardle et al. 2004; Wardle 2006).

Environmental effects of forest harvesting have been studied already for decades. Tree harvesting and regeneration practices have direct extensive effects on forest ecosystem through changes in e.g. plant cover, microclimate, distribution of organic matter, nutrient mineralization and soil compaction (Marshall 2000). Consequently, various forest regeneration methods have been shown to have some (mainly negative) effects on soil decomposer communities, although at least the decomposers of the coniferous forest soils seem to be rather well buffered against habitat changes resulting from the forestry (Siira-Pietikäinen et al. 2001; Berch et al. 2007). For example, Siira-Pietikäinen et al. (2001) found that soil microbial community structure changed in the first year, and microbial biomass and basal respiration decreased in the second year after the traditional clear felling. However, in the same experimental stands, collembolans did not respond to the forest harvestings. According to Berch et al. (2007) no differences in the mite and collembolan densities were found in the upper mineral soil among untreated, burned and scalped sites. On the other hand, clear-cutting often decimates the epiedaphic insect populations of old-growth forests, but it seems that local invertebrate species richness may even increase as forest generalists persist and many open-habitat

101 species appear at the site after logging (Niemelä 1997). In addition, Nittérus et al. (2007)
102 found out that slash removal further increased the number of generalist species of
103 carabid beetles 5-7 years after the clear-cutting.

104 In Finland, increasing amounts of forest biomass is used to produce renewable
105 energy. Forest-derived fuels used as woodchips consist mainly of logging residues such
106 as branches and small trees from thinnings and management of young stands. At present,
107 also stumps and main roots from regeneration felling areas are used to increase the
108 forest fuel production (Halonen 2004; Laitila et al. 2008). Stumps are removed mainly
109 from Norway spruce (*Picea abies*) dominated clear felled stands (Halonen 2004), as
110 well as from the clear-cuts stricken by butt rot (e.g. *Heterobasidion sp.*) to avoid
111 infection of the next tree generation (Thies and Westlind 2005; Müller et al. 2007;
112 Zabowski et al. 2008). Stump removal is a rather novel method to obtain forest biomass,
113 and its effects on the structure and functioning of diverse soil decomposer community
114 are still unexplored.

115 This study was addressed to compare the short-term responses of soil decomposer
116 communities between traditionally prepared clear-cutting areas and those where also
117 tree stumps were harvested. The experimental stands were derived from common
118 commercial clear-cuts that embodied both stump removal and traditionally site prepared
119 subareas. We sampled the intact forest floor, i.e. the patches that remained untouched
120 during the stump removal or the site preparation procedures. During the first years after
121 the soil treatments, these patches offer the only suitable habitats for soil decomposers in
122 an otherwise harsh environment of newly exposed mineral soil (Bengtsson et al. 1998;
123 Rantalainen et al. 2004). These forest floor patches are also potential sources for later
124 colonization of mineral soil along with the accumulation of new organic matter (Siira-
125 Pietikäinen et al. 2003a). In addition, the amount and size of these intact patches are

obviously different in different treatments. Specifically we focused on dominant decomposers in boreal coniferous forests: soil microflora, nematodes, enchytraeids, collembolans and macroarthropods. These organisms also represent the full range of habitat scales of decomposers and thus, may be differently affected by the additional disturbance caused by the stump removal.

Materials and Methods

Study sites and experimental design

The study sites were located in central Finland, in four regions: Juupavaara (61°52´N, 24°36´E), Haukilahti (61°48´N, 24°47´E), Jyväskylä (62°12´N, 25°40´E) and Lievestuore (62°15´N, 26°12´E). Annual mean temperature in the area is 4.3 °C, and mean annual precipitation is 642 mm. The snow cover lasts approximately four and a half months (Finnish Meteorological Institute). Soil is podzolised moraine with a 3-4 cm thick organic layer.

Fifteen Norway spruce (*Picea abies*) dominated forest stands were selected for the study. Five of these stands were clear felled in 2001, 5 in 2002 and the rest 5 in 2004. After clear felling, ca. 70% of the felling residues were collected from the sites, and stumps were removed from most of the areas using an excavator furnished with a special bucket. In the remaining area at each site, soil was prepared by mounding. One and a half year old Norway spruce seedlings from a nursery were planted at the sites except one site which was planted with larch seedlings (*Larix* sp.). All the management and regeneration practices performed in the study areas were done according to the prevailing instructions followed in forestry in Finland at that moment. Total areas of the clear felled stands varied between 0.5 and 4.5 hectares. From each site, two ca. 20 m x

20 m (400 m^2) plots were chosen for soil samplings, avoiding marshy, rocky and stony areas. One plot was in the area where stumps were collected and another in the area where stumps were left on site. The distance between the plots was more than 30 m. Altogether 30 plots were studied and the number of replicates in each treatment (stumps removed or left on site) and time (regeneration year) combination was 5. The plots with stumps were considered as controls. The proportional areas of undisturbed and mineral soil surfaces were visually estimated on each plot. Soil surface consisting of mixed mineral and organic matter was classified as mineral soil surface.

Sampling

Sampling was carried out twice in 2005. Four soil samples in May and three soil samples in September were separately taken for enchytraeid worms and collembolans. All samples were taken randomly from undisturbed forest floor from each study plot to a depth of 4 cm from the top of the litter layer including the whole organic layer with a steel soil auger (25 cm^2). At both sampling occasions, four soil samples were also taken from each plot to form one ca. 0.5 L composite sample for extraction of nematodes and for analyses of microbial community. In addition, two 25 cm x 25 cm (625 cm^2) soil samples including soil organic layer and forest floor vegetation were taken randomly from every study plot for extraction of macroarthropods. All samples were placed in plastic bags, and transported in cool boxes to the laboratory where they were stored at +5 ºC until further treated or analyzed.

Analyses and extractions

Enchytraeids were extracted from fresh soil samples for four hours using the standard wet funnel method (O'Connor 1962), and counted. The mean of the samples of each study plot for each sampling was used in the statistical analyses.

Collembolans were extracted for at least 1 week, until the samples were dry, using high-gradient extractor (dry funnels) in which temperature was continuously controlled. After extraction, animals were stored in 70% ethanol. Because the numbers of collembolans in the samples were very high, the first one hundred specimens in each sample were identified to species and the rest of the animals were counted and divided to the species in the ratios amongst the first hundred specimens. When new species were found during the counting, they were identified and added to the species list of the sample. The total pooled number of collembolans over all samples for each plot and sampling occasion was used in the analyses.

The composite soil samples were first sieved with a 4-mm mesh, and nematodes, soil moisture and soil organic matter content were determined. Nematodes were extracted for at least 13 hours from 5 g subsamples using the standard wet funnel method (O'Connor 1962), and counted. Soil moisture content was calculated after the subsamples had been dried more than 24 hours at +80 ºC. The proportion of soil organic matter was determined as loss on ignition by heating subsamples at +550 ºC for four hours. The rest of the composite soil samples that was not used in previously mentioned analyses was stored at -20 ºC for the analyses of microbial community.

Macroarthropods were extracted using large dry funnels (described by Huhta 1972). After extraction the animals were preserved in 70% ethanol and identified to family or order level depending on animal group. In addition, macroarthropods were classified to functional groups according to their feeding habits (see Persson et al. 1980). Herbivores included Aphididae, Coccoidea, Thysanoptera, Symphyta (Hymenoptera), Homoptera,

Psylloidea, Curculionidae, Elateridae and Lepidoptera; microbivores large collembolans (Entomobryidae); microbi-detritivores Protura, and larvae of Brachycera and Nematocera; and predators Araneae, Opiliones, Chilopoda, Neuroptera, Formicidae and most carabid beetles.

Microbial community structure was determined using phospholipid fatty acid (PLFA) profiles. PLFA profile was determined for each sample following procedures described by Frostegård et al. (1993) and modified by Pennanen et al. (1999). The sum of all identified PLFAs was used to indicate the total microbial biomass. The sum of PLFAs considered to be predominantly of bacterial origin (i15:0, a15:0, i16:0, 16:1ω9, 16:1ω7t, i17:0, a17:0, 17:0, cy17:0, 18:1ω7 and cy19:0) was used as an index of the bacterial biomass (PLFAbact) (Frostegård and Bååth 1996). The quantity of 18:2ω6 was used as an indicator of fungal biomass (PLFAfung), since 18:2ω6 in soil is known to be of mainly fungal origin (Federle 1986) and it is known to correlate with the amount of ergostrerol (Frostegård and Bååth 1996), a compound found only in fungi. The ratio of PLFAfung/ PLFAbact was used as an index of the ratio of fungal/bacterial biomass in the soil.

Statistical analyses

Effects of stump removal on the total numbers of nematodes, enchytraeids, collembolans and macroarthropods, microbial biomasses and soil properties as compared to the plots where stumps were left on site were tested using paired samples T-test. In addition, the numbers of soil invertebrates were analyzed using repeated measures analysis of variance (ANOVA) to find out differences between the spring and autumn samplings and between the different management years (effect of time elapsed since the treatments). These analyses were done separately for the treatments. For the

224 collembolan community in each study plot, the Shannon-Wiener diversity index (H´)
225 was calculated. Effects of the treatments on the diversity index values were tested using
226 paired samples T-test. In all statistical analyses the mean of the replicate samples
227 represented each study plot. The data analyses for the decomposer animals were
228 performed using SPSS 13.0 for Windows^{TM}.
229 To analyze the treatment effects on microbial community, the PLFAs, principal
230 component analysis (PCA) (PC-ORD 5.10 software; McCune and Mefford 1999) was
231 used.
232
233 **Results**
234
235 *Enchytraeids*
236 *Cognettia sphagnetorum* was the dominating species of enchytraeids, it
237 encompassed 99.3% in spring and 99.9% in autumn of the total numbers of enchytraeid
238 worms. Another species, *Enchytraeus flavus*, was found only in few occasional samples,
239 and it was excluded from the analyses. The numbers of *C. sphagnetorum* did not differ
240 between the treatments (Table 1, Fig. 1), but they increased from spring to autumn in
241 every treatment combination (stumps retained: $F = 23.0$; $p < 0.001$; stumps removed: F
242 $= 42.1$; $p < 0.001$).
243
244 Fig. 1.
245
246 *Nematodes*
247 The abundance of nematodes of autumn samples was significantly lower in the
248 stump removal plots only in the third year after the treatments (Table 1) compared to the

stump retaining plots. The numbers of nematodes increased during summertime one and three years after the treatments but only in the traditionally prepared plots (stumps retained: $F = 17.8$; $p < 0.001$; stumps removed: $F = 2.67$; $p = 0.128$).

Table 1.

Collembolans

Stump removal affected collembolan density when three years had elapsed since the treatments (Table 1, Fig. 2). The total numbers of collembolans were smaller in the plots where stumps were removed than in the traditionally regenerated plots in springtime. In autumn there was no effect.

Three years after the treatments, on spring sampling, *Isotomiella minor* was the only collembolan species that was affected by the stump removal: its numbers were higher in the plots where stumps were retained ($t = 4.43$, $p = 0.011$). In the autumn the difference had disappeared. The responses of *I. minor* also explain the difference in the total numbers of collembolans since it was the most abundant species in the plots. Other abundant collembolan species (*Isotoma notabilis, Folsomia quadrioculatus, Micraphorura absoloni, Pseudanurophorus septentrionalis, Pseudanurophorus binoculatus, Micranurida pygmaea* and *Mesaphorura* spp.) did not differ between the stump removal and site prepared plots (p-values > 0.05).

According to the Shannon-Wiener diversity index values, the biodiversity of collembolan communities did not differ between the differently treated study plots ($p > 0.05$; Table 2).

Table 2, Fig. 2.

Macroarthropods

There were no differences in the total numbers of macroarthropods between the plots where stumps were removed and where they were retained (p-values > 0.05; Table 1, Fig. 3). Herbivorous animals were not affected by the stump removal. Instead, there were differences between the treatments in all other functional groups: microbivorous, microbi-detritivorous and predatory macroarthropods.

In the autumn sampling microbivores were more abundant in the traditionally prepared study plots than in the stump removal plots one year after the treatments (t = 3.05; p = 0.038) resulting from the increase during the summer (F = 18.6; p = 0.001; Fig. 3).

In the spring sampling, there were more microbi-detritivores in the stump removal than in the site prepared plots three years after the treatments (t = -3.67; p = 0.021). In the autumn sampling there were no differences. Microbi-detritivores decreased between the spring and autumn samplings in the stump removal plots (F = 5.95; p = 0.031) but not in the plots where stumps were retained (F = 0.582; p = 0.46; Fig. 3).

Although predators were not affected by the treatments, their numbers increased during the summer in the stump removal plots (F = 7.08; p = 0.021) but not in the site prepared plots (F = 1.23; p = 0.289; Fig. 3).

Fig. 3.

Soil microbes and soil properties

The microbial community structure did not change due to the stump removal according to the PCA. The first five axes explained 54% of the PLFA variation, but as

no treatment effect was found on any axis the first two principal components are presented in Fig. 4. The microbial biomass (as indicated by PLFAs) did not vary much among different treatment combinations. In the autumn sampling, the total microbial and bacterial biomasses were higher in the stump removal than traditionally treated plots four years after the treatments (Table 3). In the spring sampling the fungal biomass and the ratio of fungal/bacterial biomass (PLFAfung/PLFAbact) were higher in the stump retaining than the stump removal plots one year after the treatments. In addition, the fungal/bacterial biomass ratio was somewhat higher in the stump removal plots three years after the treatments in the spring sampling (Table 3). In general, total, bacterial and fungal biomasses decreased with the aging of the plots ($F \geq 4.41$, $p \leq 0.037$), while seasonal variations were inconsistent.

The soil organic matter content did not differ between any of the treatment combinations (p-values > 0.05), the mean being in the site prepared plots 70±7.4% (mean±S.E.) and in the stump removal plots 66.2±6.6%. Nor did the soil water content differ between the treatments (p-values > 0.05), the mean was 65.5±4.3% in the traditionally managed plots and 63.5±3.0% in the stump removal plots. The proportions of undisturbed forest floor in the stump removal plots were significantly lower than those in stump retaining plots (one year after the treatments $t = 4.32$, $p = 0.012$; three years after $t = 7.30$, $p = 0.002$; and four years after $t = 16.0$, $p < 0.001$). The mean proportions of undisturbed forest floor in stump removal and stump retaining plots were 28±4.6% and 63.7±3.2%, respectively.

Table 3, Fig. 4.

Discussion

Our study showed that the stump removal from boreal coniferous forest clear-cut areas, performed as in routine forestry in Finland, does not induce further drastic and consistent changes in the decomposer community of undisturbed forest floor when compared to the traditionally prepared areas. Only some minor changes in soil microbe and animal abundances were observed due to the stump pulling procedure. This indicates a resistance of the decomposer community since lots of resources are lost from the ecosystem and the soil habitat is greatly changed along with the stump removal. For example, almost as much wood is removed from the stands in logging residues and stumps as in the harvested stems (Palviainen 2005). The stump removal also reduced the amount of intact forest floor that is the habitat of good quality available for decomposers. In addition, the results indicated that the size of habitat range does not necessarily determine the level of response of the organism to the stump removal.

When stumps are removed from the forest, the major part of soil organic layer is seriously disturbed, turned upside down or mixed to the mineral soil. At our study sites, the area of undamaged forest floor in the stump removal areas was only half of that in the traditionally managed areas. This fact evidently affects the overall impact of the stump removal at forest stand level. Although Rantalainen et al. (2008) found that soil decomposer community is insensitive to habitat fragmentation, it has been shown that organic matter removal can affect the soil food web over decades (Bengtsson et al. 1998). Exposed mineral soil is a hostile environment for most soil fauna (see e.g. Siira-Pietikäinen et al. 2003a). Thus, in the stump removal areas there is much less habitat of high quality available for decomposers than in traditionally prepared areas. At the forest stand level, this leads to smaller and more fragmented populations of decomposers in the stump removal areas. Although the soil organic layer is not totally removed from the

area along site preparation and stump removal, most of it is of lower quality for decomposers as covered by mounds of mineral soil or dispersed to mineral soil.

Most of the nutrients in dead organic matter are mineralized by soil microbes (e.g. Wardle et al. 2004). Forest management practices have shown to have either negative (Pietikäinen and Fritze 1995) or negligible (Smolander et al. 1998; Siira-Pietikäinen et al. 2001) effects on coniferous forest soil microbes. Our study showed – at least in short-term – that patches of forest floor in the stump removal areas harbor similar microbial communities compared to patches in the traditionally prepared areas. In addition, observed changes in microbial biomasses were only small and transient.

In the present study, nematodes were one of the few soil faunal groups that were affected negatively by the stump removal. The difference between the treatments might not have been due to the soil moisture, amount of organic matter or microbial community structure (bottom-up) because no clear changes were observed in these parameters between the stump removal and traditionally prepared areas. Because the response was short-term (in autumn only) and transient (the third year only), its impact on soil processes is likely to be negligible.

Although it has been shown that forest management practices change the arthropod community compared to mature forests, the disturbance has not seemed to be very effective in the soil (Greenberg and McGrane 1996). In our study, the total numbers of epiedaphic macroarthropods were insensitive to the stump removal. However, at functional group level (classified by the feeding behavior) some transient differences between the stump removal and stump retaining plots were detected. Microbivores, large collembolans living on the soil surface in our forests, were more abundant already one year after the treatments in the traditionally prepared areas. These arthropods may derive large part of their nutrition from plant tissues (Chahartaghi et al. 2005), and thus

smaller amount of intact forest floor in the stump removal areas evidently reduced their resources soon after the treatments. On the other hand, microbi-detritivores, majority being larvae of dipterans, responded positively to the stump removal three years after the treatments. High abundance of these larvae in the stump removal areas may simply be due to less available intact forest floor for adult insects to lay eggs. In the autumn their abundances were leveled out, most obviously due to emergence of adults. All the observed responses among macroarthropods were short-term, and that is why their ecological consequences obviously remained negligible.

Our results indicated that although there were less undamaged forest floor available as habitats for soil decomposers in the stump removal areas, these fragments harbored quite similar communities compared to the fragments in the traditionally prepared sites. There is also previous evidence that soil fauna of coniferous forests is quite insensitive to clear felling and other stand management practices (e.g. Setälä et al. 2000; Siira-Pietikäinen et al. 2001; Siira-Pietikäinen et al. 2003b). Setälä et al. (2005) pointed out that soil is a very heterogeneous environment in small spatial scale. Thus, resource competition between taxa is reduced in soils allowing a co-existence of species with similar dietary requirements. At least in short-term, fragments in the stump removal areas seem to be frequent and large enough to act as suitable habitats for decomposer organisms of different sizes with different habitat ranges and biology. In addition, these fragments may act as refugia for organisms and consequently as sources for colonization when organic matter accumulation makes exposed mineral soil areas suitable habitats for decomposers (Siira-Pietikäinen et al. 2003a).

The heterogeneity of forest soils was challenging our sampling procedure. The number of replicates was quite low (five), but the representativeness of our samples was increased by taking randomly several samples from each plot. In addition, the effect of

399 the heterogeneity on our results was reduced by using the paired experimental set-up; i.e.
400 both treatments were performed in each clear-cut.

401 Stump removal is a rather new forestry practice and its effects on forest ecosystem
402 and next tree generations are still poorly known. Large amounts of nutrients and carbon
403 are lost from forest along and soon after clear felling (Palviainen et al. 2004). This loss
404 is evidently larger when also logging residues and stumps with main roots are removed
405 from the clear-felled areas. Particularly, these materials form a long-term source of
406 carbon and nutrients in clear-cut coniferous forests. Melin et al. (2009) estimated that it
407 takes 64 years before 95% of the spruce stumps and roots are decomposed in boreal
408 forests. On the other hand, podzolized soil profile with thick humus layer of coniferous
409 forests has developed during hundreds of years, and redistribution of these layers may
410 have serious impacts on the fate of old organic carbon and nutrients. Soil organic matter
411 has an important role in the site productivity since it affects e.g. bulk density, water
412 holding capacity, microbial populations and cation-exchange capacity of the soil
413 (Johnson 1992). It has already been shown that the whole tree harvesting affect
414 negatively the second rotation forest productivity when only above ground biomass was
415 removed (Walmsley et al. 2009).

416 In many countries the usage of renewable energy sources is continuously
417 increasing, e.g. the production of forest chips in Finland was raised from 1.7 million m^3
418 in 2002 to 5 million m^3 in 2010 (Hakkila 2006, Finnish Forest Research Institute 2009).
419 This means intensification of the forestry, and increasing amount of forest biomass will
420 be required to achieve the goals. Thus, there is an urgent need to study also the
421 development of exposed and otherwise disturbed soil patches in the stump removal
422 areas to fully understand the forest stand scale consequences of stump removal.
423

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Table 1. Abundances (mean ± S.E.) of different animal groups in 2005, one, three and four years after the treatments. Significant differences between stump removal and traditional site preparation are indicated by $p < 0.05$.

Animal Group	Treatment Year	Sampling Time 2005	Stump Removal	Mean	S.E.	Paired Samples T-Test *t*	*p*
Enchytraeids[a]	2001	spring	yes	27100	7560	0.77	0.48
			no	33780	8468		
		autumn	yes	58667	17757	0.82	0.46
			no	75120	9225		
	2002	spring	yes	31560	4269	-1.39	0.24
			no	23560	4965		
		autumn	yes	124187	9617	-0.31	0.77
			no	111227	36891		
	2004	spring	yes	35113	10091	-0.7	0.53
			no	27427	5021		
		autumn	yes	95760	22467	-0.8	0.45
			no	81680	11455		
Nematodes[b]	2001	spring	yes	20	6.0	1.03	0.36
			no	24	3.5		
		autumn	yes	29	5.5	0.31	0.77
			no	32	6.2		
	2002	spring	yes	23	6.0	-0.6	0.58
			no	18	5.6		
		autumn	yes	30	4.2	3.47	**0.03**
			no	67	12		
	2004	spring	yes	32	6.7	0.84	0.45
			no	37	5.2		
		autumn	yes	38	12	1.7	0.16
			no	71	16		
Collembolans[a]	2001	spring	yes	20580	6790	0.19	0.86
			no	22360	4360		
		autumn	yes	53200	7747	-1.15	0.32
			no	46027	8010		
	2002	spring	yes	25380	6458	2.93	**0.04**
			no	40120	8776		
		autumn	yes	34613	5003	0.13	0.9
			no	35600	3602		
	2004	spring	yes	33060	8562	0.72	0.51
			no	40220	11611		
		autumn	yes	58267	22287	-0.44	0.68
			no	45227	9115		
Macroarthropods[a]	2001	spring	yes	3221	414	-1.78	0.15
			no	3385	536		
		autumn	yes	6016	818	0.16	0.88
			no	6186	1024		
	2002	spring	yes	4228	824	0.79	0.47
			no	5074	1137		
		autumn	yes	7844	1565	0.3	0.78
			no	9320	2257		
	2004	spring	yes	1758	723	-1.54	0.2
			no	2758	1550		
		autumn	yes	3300	1361	2.2	0.09
			no	4905	2729		

[a] individuals/m^2

[b] individuals/1g dw soil

Table 2. Shannon-Wiener diversity indices (*H'*) for Collembolan community in 2005, one, three and four years after the treatments (n = 5).

Treatment Year	Sampling Time	Stump Removal	Mean H'	S.E.
2001	spring	yes	1.85	0.13
		no	2.01	0.12
	autumn	yes	1.98	0.10
		no	2.02	0.19
2002	spring	yes	2.00	0.18
		no	1.88	0.11
	autumn	yes	2.09	0.08
		no	2.12	0.07
2004	spring	yes	1.75	0.09
		no	1.66	0.13
	autumn	yes	1.94	0.05
		no	2.00	0.03

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Table 3. Microbial biomass indicator values (mean ± S.E.) in 2005, one, three and four years after the treatments. Significant differences between stump removal and traditional site preparation are indicated by $p < 0.05$.

Microbe Group	Treatment Year	Sampling Time 2005	Stump Removal	Mean	S.E.	Paired Samples T-Test *t*	*p*
Total biomass[a]	2001	spring	yes	2296	607	-0.06	0.96
			no	2254	235		
		autumn	yes	1784	65.1	-3.64	**0.02**
			no	1399	56.1		
	2002	spring	yes	2520	472	0.06	0.96
			no	2541	311		
		autumn	yes	2396	139	-2.32	0.08
			no	1694	262		
	2004	spring	yes	1721	140	1.08	0.34
			no	1951	215		
		autumn	yes	2077	238	1.08	0.34
			no	2290	199		
Bacterial biomass[a]	2001	spring	yes	861	236	-0.06	0.95
			no	843	97.5		
		autumn	yes	652	30.1	-2.81	**0.05**
			no	506	25.1		
	2002	spring	yes	955	202	0.35	0.74
			no	1006	137		
		autumn	yes	944	75.3	-2.4	0.08
			no	657	102		
	2004	spring	yes	668	64.5	0.64	0.56
			no	714	78.5		
		autumn	yes	768	37.5	0.84	0.45
			no	835	86.2		
Fungal biomass[a]	2001	spring	yes	104	19	0.43	0.69
			no	115	12		
		autumn	yes	114	7.7	-1.66	0.17
			no	92	6.3		
	2002	spring	yes	125	20	-1.05	0.35
			no	97	15		
		autumn	yes	96	7.9	-0.67	0.54
			no	80	16		
	2004	spring	yes	63	9.8	2.7	**0.05**
			no	120	16		
		autumn	yes	120	18	1.83	0.14
			no	157	20		
PLFAfung/ PLFAbact	2001	spring	yes	0.13	0.016	0.45	0.68
			no	0.14	0.003		
		autumn	yes	0.18	0.021	0.22	0.84
			no	0.19	0.021		
	2002	spring	yes	0.14	0.016	-2.71	**0.05**
			no	0.1	0.014		
		autumn	yes	0.1	0.012	0.5	0.64
			no	0.12	0.014		
	2004	spring	yes	0.1	0.015	3.66	**0.02**
			no	0.17	0.01		
		autumn	yes	0.15	0.017	1.52	0.2
			no	0.19	0.028		

[a] nmol PLFA g^{-1} organic matter

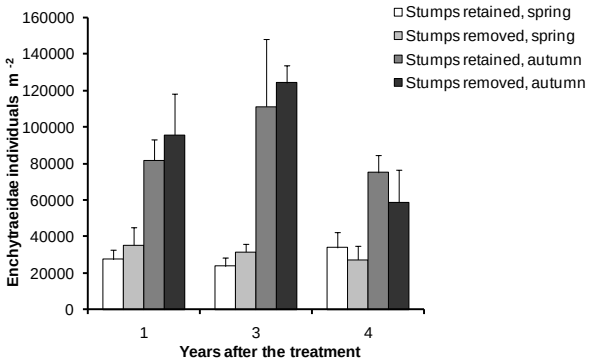
Figure legends:

Figure 1. Total numbers of enchytraeids (inds m^{-2}, mean + S.E.) in differently treated study sites one, three and four years after the treatment (n = 5).

Figure 2. Total numbers of Collembolans (inds m^{-2}, mean + S.E.) in differently treated study sites one, three and four years after the treatment (n = 5).

Figure 3. The numbers of macroarthropods in total, predators, herbivores, microbivores and microbi-detritivores (inds m^{-2}, mean + S.E.) in differently treated study sites one, three and four years after the treatment (n = 5).

Figure 4. Principal component (PCA) scores for phospholipid fatty acid (PLFA) data for differently treated study sites one, three and four years after the treatment (n = 5). Small symbols refer to spring and large symbols to autumn sampling, respectively.



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576 Figure 1. Total numbers of enchytraeids (inds m^{-2}, mean + S.E.) in differently treated

577 study sites one, three and four years after the treatment (n = 5).

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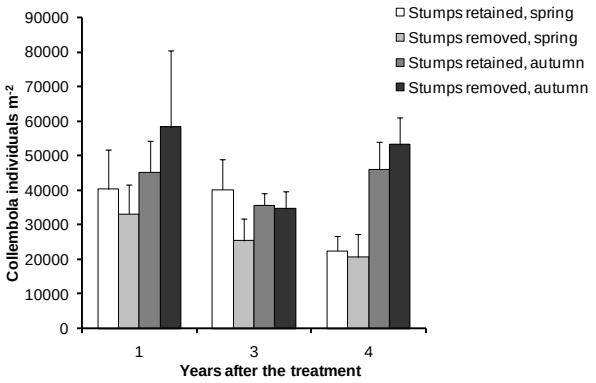

579

580 Figure 2. Total numbers of Collembolans (inds m^{-2}, mean + S.E.) in differently treated

581 study sites one, three and four years after the treatment (n = 5).

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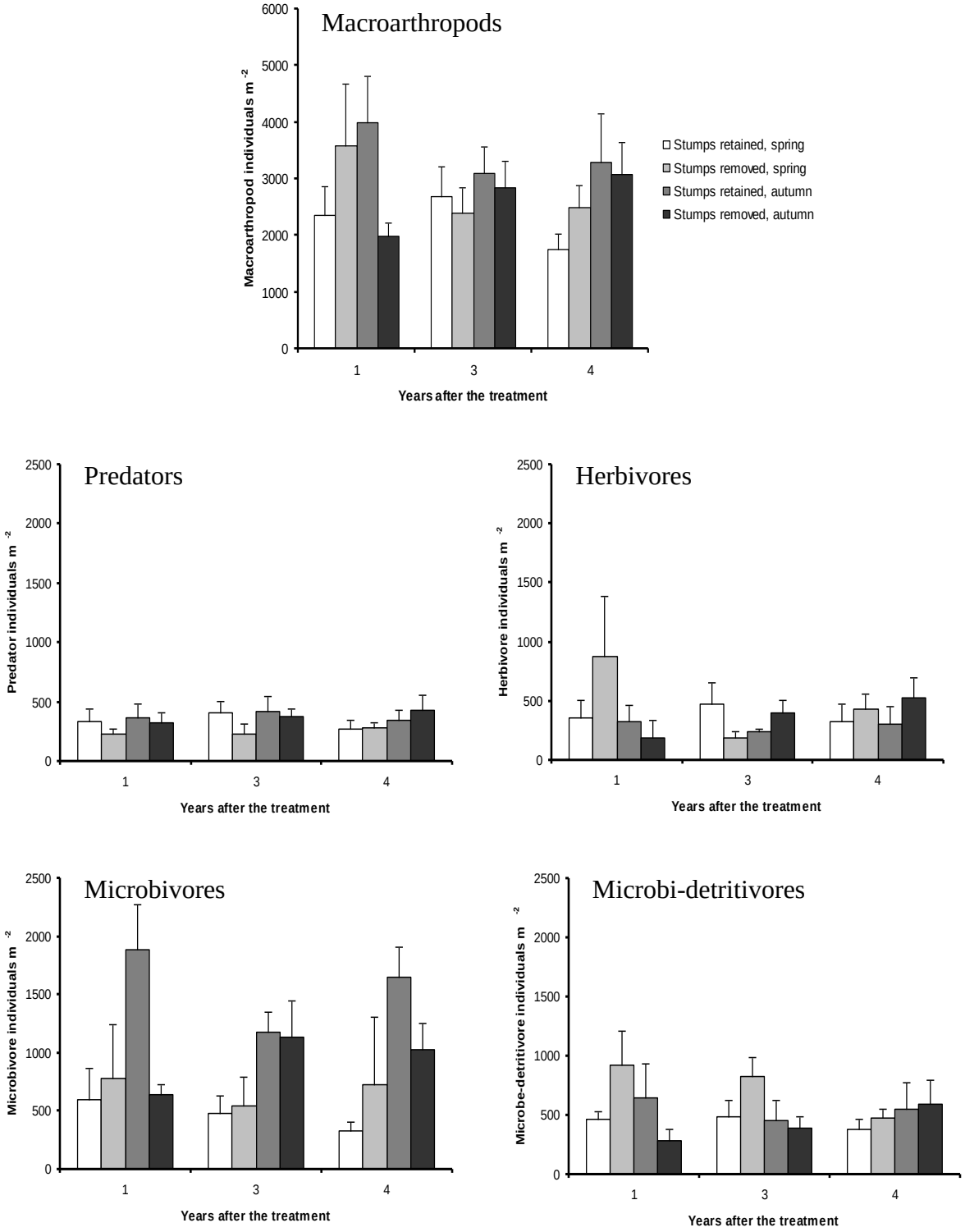
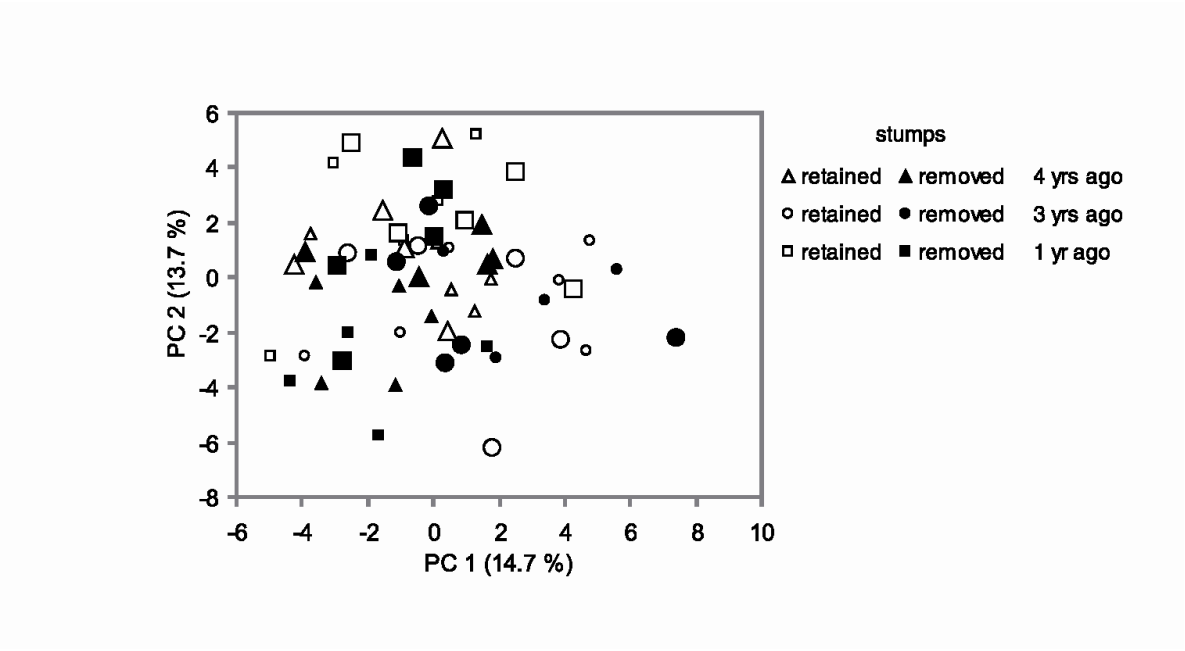


Figure 3. The numbers of macroarthropods in total, predators, herbivores, microbivores and microbi-detritivores (inds m^{-2}, mean + S.E.) in differently treated study sites one, three and four years after the treatment (n = 5).



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628 Figure 4. Principal component (PCA) scores for phospholipid fatty acid (PLFA) data for
629 differently treated study sites one, three and four years after the treatment (n = 5). Small
630 symbols refer to spring and large symbols to autumn sampling, respectively.

631