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

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44

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

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52 **Introduction**

53

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

64 In general, soil organisms seem to be rather resistant to habitat fragmentation
65 (Rantalainen et al. 2008). The habitat scale of decomposers is usually smaller than that
66 of aboveground fauna depending, however, on the body sizes, mobility and territory
67 sizes of the organisms. As forest soil is usually heterogeneous, even a small area can
68 provide suitable habitats and resources for numerous organisms. For example, a square
69 meter of boreal forest soil can be inhabited on average by 2.4 millions of nematodes,
70 50 000 enchytraeid worms and 80 000 collembolans (Huhta et al. 1986), and ca. 94 000
71 km fungal hyphae (calculated from Persson et al. 1980) and $10\text{-}15 \times 10^{13}$ cells of
72 bacteria (Persson et al. 1980). Thus, it is important to bear in mind that habitat sizes and
73 diversity patterns differ significantly between above- and belowground communities,
74 the diversity appearing to be very context dependent (De Deyn and Van der Putten
75 2005).

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

85 Environmental effects of forest harvesting have been studied already for decades.
86 Tree harvesting and regeneration practices have direct extensive effects on forest
87 ecosystem through changes in e.g. plant cover, microclimate, distribution of organic
88 matter, nutrient mineralization and soil compaction (Marshall 2000). Consequently,
89 various forest regeneration methods have been shown to have some (mainly negative)
90 effects on soil decomposer communities, although at least the decomposers of the
91 coniferous forest soils seem to be rather well buffered against habitat changes resulting
92 from the forestry (Siira-Pietikäinen et al. 2001; Berch et al. 2007). For example, Siira-
93 Pietikäinen et al. (2001) found that soil microbial community structure changed in the
94 first year, and microbial biomass and basal respiration decreased in the second year after
95 the traditional clear felling. However, in the same experimental stands, collembolans did
96 not respond to the forest harvestings. According to Berch et al. (2007) no differences in
97 the mite and collembolan densities were found in the upper mineral soil among
98 untreated, burned and scalped sites. On the other hand, clear-cutting often decimates the
99 epiedaphic insect populations of old-growth forests, but it seems that local invertebrate
100 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

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

131

132 **Materials and Methods**

133

134 *Study sites and experimental design*

135 The study sites were located in central Finland, in four regions: Juupavaara
136 (61°52'N, 24°36'E), Haukilahti (61°48'N, 24°47'E), Jyväskylä (62°12'N, 25°40'E) and
137 Lievestuore (62°15'N, 26°12'E). Annual mean temperature in the area is 4.3 °C, and
138 mean annual precipitation is 642 mm. The snow cover lasts approximately four and a
139 half months (Finnish Meteorological Institute). Soil is podzolised moraine with a 3-4
140 cm thick organic layer.

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

151 20 m (400 m²) plots were chosen for soil samplings, avoiding marshy, rocky and stony
152 areas. One plot was in the area where stumps were collected and another in the area
153 where stumps were left on site. The distance between the plots was more than 30 m.
154 Altogether 30 plots were studied and the number of replicates in each treatment (stumps
155 removed or left on site) and time (regeneration year) combination was 5. The plots with
156 stumps were considered as controls. The proportional areas of undisturbed and mineral
157 soil surfaces were visually estimated on each plot. Soil surface consisting of mixed
158 mineral and organic matter was classified as mineral soil surface.

159

160 *Sampling*

161 Sampling was carried out twice in 2005. Four soil samples in May and three soil
162 samples in September were separately taken for enchytraeid worms and collembolans.
163 All samples were taken randomly from undisturbed forest floor from each study plot to
164 a depth of 4 cm from the top of the litter layer including the whole organic layer with a
165 steel soil auger (25 cm²). At both sampling occasions, four soil samples were also taken
166 from each plot to form one ca. 0.5 L composite sample for extraction of nematodes and
167 for analyses of microbial community. In addition, two 25 cm x 25 cm (625 cm²) soil
168 samples including soil organic layer and forest floor vegetation were taken randomly
169 from every study plot for extraction of macroarthropods. All samples were placed in
170 plastic bags, and transported in cool boxes to the laboratory where they were stored at
171 +5 °C until further treated or analyzed.

172

173 *Analyses and extractions*

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

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

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

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

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

203 Microbial community structure was determined using phospholipid fatty acid
204 (PLFA) profiles. PLFA profile was determined for each sample following procedures
205 described by Frostegård et al. (1993) and modified by Pennanen et al. (1999). The sum
206 of all identified PLFAs was used to indicate the total microbial biomass. The sum of
207 PLFAs considered to be predominantly of bacterial origin (i15:0, a15:0, i16:0, 16:1 ω 9,
208 16:1 ω 7t, i17:0, a17:0, 17:0, cy17:0, 18:1 ω 7 and cy19:0) was used as an index of the
209 bacterial biomass (PLFAbact) (Frostegård and Bååth 1996). The quantity of 18:2 ω 6 was
210 used as an indicator of fungal biomass (PLFAfung), since 18:2 ω 6 in soil is known to be
211 of mainly fungal origin (Federle 1986) and it is known to correlate with the amount of
212 ergosterol (Frostegård and Bååth 1996), a compound found only in fungi. The ratio of
213 PLFAfung/ PLFAbact was used as an index of the ratio of fungal/bacterial biomass in
214 the soil.

215

216 *Statistical analyses*

217 Effects of stump removal on the total numbers of nematodes, enchytraeids,
218 collembolans and macroarthropods, microbial biomasses and soil properties as
219 compared to the plots where stumps were left on site were tested using paired samples
220 T-test. In addition, the numbers of soil invertebrates were analyzed using repeated
221 measures analysis of variance (ANOVA) to find out differences between the spring and
222 autumn samplings and between the different management years (effect of time elapsed
223 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™.

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

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

252

253 Table 1.

254

255 *Collembolans*

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

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

269 According to the Shannon-Wiener diversity index values, the biodiversity of
270 collembolan communities did not differ between the differently treated study plots ($p >$
271 0.05 ; Table 2).

272

273 Table 2, Fig. 2.

274

275 *Macroarthropods*

276 There were no differences in the total numbers of macroarthropods between the
277 plots where stumps were removed and where they were retained (p -values > 0.05 ; Table
278 1, Fig. 3). Herbivorous animals were not affected by the stump removal. Instead, there
279 were differences between the treatments in all other functional groups: microbivorous,
280 microbi-detritivorous and predatory macroarthropods.

281 In the autumn sampling microbivores were more abundant in the traditionally
282 prepared study plots than in the stump removal plots one year after the treatments ($t =$
283 3.05 ; $p = 0.038$) resulting from the increase during the summer ($F = 18.6$; $p = 0.001$; Fig.
284 3).

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

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

293

294 Fig. 3.

295

296 *Soil microbes and soil properties*

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

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

310 The soil organic matter content did not differ between any of the treatment
311 combinations (p -values > 0.05), the mean being in the site prepared plots $70 \pm 7.4\%$
312 (mean \pm S.E.) and in the stump removal plots $66.2 \pm 6.6\%$. Nor did the soil water content
313 differ between the treatments (p -values > 0.05), the mean was $65.5 \pm 4.3\%$ in the
314 traditionally managed plots and $63.5 \pm 3.0\%$ in the stump removal plots. The proportions
315 of undisturbed forest floor in the stump removal plots were significantly lower than
316 those in stump retaining plots (one year after the treatments $t = 4.32$, $p = 0.012$; three
317 years after $t = 7.30$, $p = 0.002$; and four years after $t = 16.0$, $p < 0.001$). The mean
318 proportions of undisturbed forest floor in stump removal and stump retaining plots were
319 $28 \pm 4.6\%$ and $63.7 \pm 3.2\%$, respectively.

320

321 Table 3, Fig. 4.

322

323 **Discussion**

324

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

337 When stumps are removed from the forest, the major part of soil organic layer is
338 seriously disturbed, turned upside down or mixed to the mineral soil. At our study sites,
339 the area of undamaged forest floor in the stump removal areas was only half of that in
340 the traditionally managed areas. This fact evidently affects the overall impact of the
341 stump removal at forest stand level. Although Rantalainen et al. (2008) found that soil
342 decomposer community is insensitive to habitat fragmentation, it has been shown that
343 organic matter removal can affect the soil food web over decades (Bengtsson et al.
344 1998). Exposed mineral soil is a hostile environment for most soil fauna (see e.g. Siira-
345 Pietikäinen et al. 2003a). Thus, in the stump removal areas there is much less habitat of
346 high quality available for decomposers than in traditionally prepared areas. At the forest
347 stand level, this leads to smaller and more fragmented populations of decomposers in
348 the stump removal areas. Although the soil organic layer is not totally removed from the

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

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

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

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

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

382 Our results indicated that although there were less undamaged forest floor
383 available as habitats for soil decomposers in the stump removal areas, these fragments
384 harbored quite similar communities compared to the fragments in the traditionally
385 prepared sites. There is also previous evidence that soil fauna of coniferous forests is
386 quite insensitive to clear felling and other stand management practices (e.g. Setälä et al.
387 2000; Siira-Pietikäinen et al. 2001; Siira-Pietikäinen et al. 2003b). Setälä et al. (2005)
388 pointed out that soil is a very heterogeneous environment in small spatial scale. Thus,
389 resource competition between taxa is reduced in soils allowing a co-existence of species
390 with similar dietary requirements. At least in short-term, fragments in the stump
391 removal areas seem to be frequent and large enough to act as suitable habitats for
392 decomposer organisms of different sizes with different habitat ranges and biology. In
393 addition, these fragments may act as refugia for organisms and consequently as sources
394 for colonization when organic matter accumulation makes exposed mineral soil areas
395 suitable habitats for decomposers (Siira-Pietikäinen et al. 2003a).

396 The heterogeneity of forest soils was challenging our sampling procedure. The
397 number of replicates was quite low (five), but the representativeness of our samples was
398 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 m³
418 in 2002 to 5 million m³ 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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432 **References**

433 Allen, M.F. (1991). *The Ecology of Mycorrhizae*. Cambridge, Great Britain: University
434 Press.

435 Bengtsson, J., Lundkvist, H., Saetre, P., Sohlenius, B., and Solbreck, B. (1998). Effects
436 of organic matter removal on the soil food web: Forestry practices meet ecological
437 theory. *Applied Soil Ecology*, 9, 137-143.

438 Berch, S.M., Battigelli, J.P., and Hope, G.D. (2007). Responses of soil mesofauna
439 communities and oribatid mite species to site preparation treatments in high-
440 elevation cutblocks in southern British Columbia. *Pedobiologia*, 51, 23-32.

441 Chahartaghi, M., Langel, R., Scheu, S., and Ruess, L. (2005). Feeding guilds in
442 Collembola based on nitrogen stable isotope ratios. *Soil Biology and Biochemistry*,
443 37, 1718-1725.

444 De Deyn, G., and Van der Putten, W. (2005). Linking aboveground and belowground
445 diversity. *Trends in Ecology and Evolution*, 20, 625-633.

446 Federle, T.W. (1986). Microbial distribution in soil - new techniques. In Megusar, F.,
447 and Gantar, M. (Eds.), *Perspectives of microbial ecology* (pp. 493-498). Slovene
448 Society of Microbiology, Ljubljana.

449 Finnish Forest Research Institute (2009). *Finnish statistical yearbook of forestry*.
450 Sastamala: Vammala Publisher. (In Finnish).

451 Frostegård, Å, Tunlid, A., and Bååth, E. (1993). Phospholipid fatty acid composition,
452 biomass, and activity of microbial communities from two soil types experimentally

453 exposed to different heavy metals. *Applied and Environmental Microbiology*, 59,
454 3605-3617.

455 Frostegård, Å., and Bååth, E. (1996). The use of phospholipid fatty acid analysis to
456 estimate bacterial and fungal biomass in soil. *Biology and Fertility of Soils*, 22, 59-
457 65.

458 Greenberg, C.H., and McGrane, A. (1996). A comparison of relative abundance and
459 biomass of ground-dwelling arthropods under different forest management
460 practices. *Forest Ecology and Management*, 89, 31-41.

461 Hakkila, P. (2006). Factors driving the development of forest energy in Finland.
462 *Biomass and Bioenergy*, 30, 281-288.

463 Halonen, M. (2004). Metsäenergiapuun hankinta [Acquisition of forest fuel wood].
464 Toimintaohje. UPM-Kymmene. 37 pp. (in Finnish)

465 Hanski, I. (1999). *Metapopulation Ecology*. New York, United States: Oxford
466 University Press.

467 Huhta, V. (1972). Efficiency of different dry funnel techniques in extracting arthropoda
468 from raw humus forest soil. *Annales Zoologici Fennici*, 9, 42-48.

469 Huhta, V., Hyvönen, R., Kaasalainen, P., Koskenniemi, A., Muona, J., Mäkelä, I.,
470 Sulander, M., and Vilkkamaa, P. (1986). Soil fauna of Finnish coniferous forests.
471 *Annales Zoologici Fennici*, 23, 345-360.

472 Huhta, V., Persson, T., and Setälä, H. (1998). Functional implications of soil fauna
473 diversity in boreal forests. *Applied Soil Ecology*, 10, 277-288.

- 474 Johnson, D.W. (1992). Effects of forest management on soil carbon storage. *Water, Air,*
475 *and Soil Pollution*, 64, 83-120.
- 476 Laakso, J., and Setälä, H. (1999). Sensitivity of primary production to changes in the
477 architecture of belowground food webs. *Oikos*, 87, 57-64.
- 478 Laitila, J., Asikainen, A., and Anttila, P. (2008). 1. Energiapuuvarat [Reserves of fuel
479 wood] . In Kuusinen, M., and Ilvesniemi, H. (Eds.), *Energiapuun Korjuun*
480 *Ympäristövaikutukset [Environmental effects of wood fuel harvesting]*,
481 Tutkimusraportti (pp. 6-12.). Tapion ja Metlan julkaisuja. Retrieved March 3, 2008
482 from www.metsavastaa.net/energiapuu/raportti (in Finnish).
- 483 Marshall, V.G. (2000). Impacts of forest harvesting on biological processes in northern
484 forest soils. *Forest Ecology and Management*, 133, 43-60.
- 485 McCune, B., and Mefford, M.J. (1999). *PC-ORD. Multivariate Analysis of Ecological*
486 *Data, Version 4*. Gleneden Beach, Oregon, United States: MjM Software Design.
- 487 Melin, Y., Petersson, H., and Nordfjell, T. (2009). Decomposition of stump and root
488 systems of Norway spruce in Sweden—A modelling approach. *Forest Ecology and*
489 *Management*, 257, 1445-1451.
- 490 Müller, M.M., Heinonen, J., and Korhonen, K. (2007). Occurrence of *Heterobasidion*
491 *basidiocarps* on cull pieces of Norway spruce left on cutting areas and in mature
492 spruce stands. *Forest Pathology*, 37, 374-386.
- 493 Niemelä, J. (1997). Invertebrates and boreal forest management. *Conservation Biology*,
494 11, 601-610.

495 Nittérus, K., Åström, M., and Gunnarsson, B. (2007). Commercial harvest of logging
496 residue in clear-cuts affects the diversity and community composition of ground
497 beetles (Coleoptera: Carabidae). *Scandinavian Journal of Forest Research*, 22,
498 231-240.

499 O'Connor, F. B. (1962). The extraction of Enchytraeidae from soil. In: Murphy, P. W.
500 (Ed.), *Progress in Soil Zoology* (pp. 279-285). Butterworths, London.

501 Palviainen, M. (2005). Logging residues and ground vegetation in nutrient dynamics of
502 a clear-cut boreal forest (Doctoral dissertation, Faculty of Forestry, University of
503 Joensuu). *Dissertationes Forestales*, 12, 1-38.

504 Palviainen, M., Finer, L., Kurka, A.M., Mannerkoski, H., Piirainen, S., and Starr, M.
505 (2004). Decomposition and nutrient release from logging residues after clear-
506 cutting of mixed boreal forest. *Plant and Soil*, 263, 53-67.

507 Pennanen, T., Liski, J., Bååth, E., Kitunen, V., Uotila, J., Westman, C.J., and Fritze, H.
508 (1999). Structure of the microbial communities in coniferous forest soils in relation
509 to site fertility and stand development stage. *Microbial Ecology*, 38, 168-179.

510 Persson, T., Bååth, E., Clarholm, M., Lundkvist, H., Söderström, B.E., and Sohlenius, B.
511 (1980). Trophic structure, biomass dynamics and carbon metabolism of soil
512 organisms in a Scots pine forest. In: Persson, T. (Ed.), *Structure and Function of*
513 *Northern Coniferous Forests – An Ecosystem Study. Ecological Bulletins*, 32, 419-
514 459. Stockholm.

515 Pietikäinen, J., and Fritze, H. (1995). Clear-cutting and prescribed burning in coniferous
516 forest: Comparison of effects on soil fungal and total microbial biomass,
517 respiration activity and nitrification. *Soil Biology and Biochemistry*, 27, 101-109.

518 Rantalainen, M., Kontiola, L., Haimi, J., Fritze, H., and Setälä, H. (2004). Influence of
519 resource quality on the composition of soil decomposer community in fragmented
520 and continuous habitat. *Soil Biology and Biochemistry*, 36, 1983-1996.

521 Rantalainen, M., Haimi, J., Fritze, H., Pennanen, T., and Setälä, H. (2008). Soil
522 decomposer community as a model system in studying the effects of habitat
523 fragmentation and habitat corridors. *Soil Biology and Biochemistry*, 40, 853-863.

524 Setälä, H., Haimi, J., and Siira-Pietikäinen, A. (2000). Sensitivity of soil processes in
525 northern forest soils: Are management practices a threat? *Forest Ecology and*
526 *Management*, 133, 5-11.

527 Setälä, H., Berg, M., and Jones, T.H. (2005). Trophic Structure and Functional
528 redundancy in Soil Communities. In Bardgett, R.D., Hopkins, D.W., and Usher, M.
529 (Eds.), *Biological Diversity and Function in Soils* (pp.236-249). Cambridge,
530 United Kingdom: University Press.

531 Siira-Pietikäinen, A., Haimi, J., and Fritze, H. (2003a). Organisms, decomposition, and
532 growth of pine seedlings in boreal forest soil affected by sod cutting and trenching.
533 *Biology and Fertility of Soils*, 37, 163-174.

534 Siira-Pietikäinen, A., Haimi, J., and Siitonen, J. (2003b). Short-term responses of soil
535 macroarthropod community to clear felling and alternative forest regeneration
536 methods. *Forest Ecology and Management*, 172, 339-353.

537 Siira-Pietikäinen, A., Pietikäinen, J., Fritze, H., and Haimi, J. (2001). Short-term
538 responses of soil decomposer communities to forest management: Clear felling
539 versus alternative forest harvesting methods. *Canadian Journal of Forest Research*,
540 *31*, 88-99.

541 Smolander, A., Priha, O., Paavolainen, L., Steer, J., and Mälkönen, E. (1998). Nitrogen
542 and carbon transformations before and after clear-cutting in repeatedly N-fertilized
543 and limed forest soil. *Soil Biology and Biochemistry*, *30*, 477-490.

544 Thies, W.G., and Westlind, D.J. (2005). Stump removal and fertilization of five
545 *Phellinus weirii*-infested stands in Washington and Oregon affect mortality and
546 growth of planted douglas-fir 25 years after treatment. *Forest Ecology and*
547 *Management*, *219*, 242-258.

548 Walmsley, J.D., Jones, D.L., Reynolds, B., Price, M.H., and Healey, J.R. (2009). Whole
549 tree harvesting can reduce second rotation forest productivity. *Forest Ecology and*
550 *Management*, *257*, 1104-1111.

551 Wardle, D. (2006). The influence of biotic interactions on soil biodiversity. *Ecology*
552 *Letters*, *9*, 870-886.

553 Wardle, D.A., Bardgett, R.D., Klironomos, J.N., Setälä, H., and van der Putten, W.H.,
554 Wall, D.H. (2004). Ecological linkages between aboveground and belowground
555 biota. *Science*, *304*, 1629-1633.

556 Zabowski, D., Chambreau, D., Rotramel, N., and Thies, W.G. (2008). Long-term effects
557 of stump removal to control root rot on forest soil bulk density, soil carbon and
558 nitrogen content. *Forest Ecology and Management*, *255*, 720-727.

Table 1. Abundances (mean \pm 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	
						<i>t</i>	<i>p</i>
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/m²

^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

Table 3. Microbial biomass indicator values (mean \pm 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	
						<i>t</i>	<i>p</i>
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

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562 Figure legends:

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

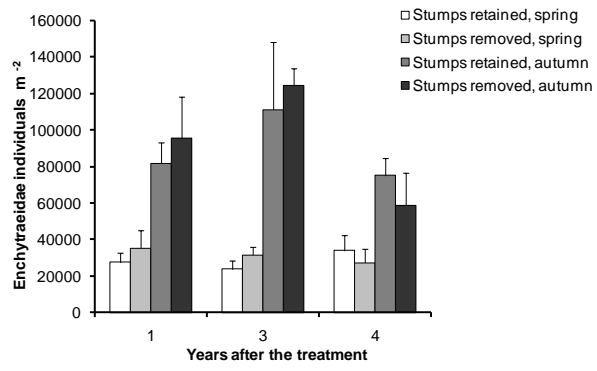
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566 Figure 2. Total numbers of Collembolans (inds m⁻², mean + S.E.) in differently treated
567 study sites one, three and four years after the treatment (n = 5).

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

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

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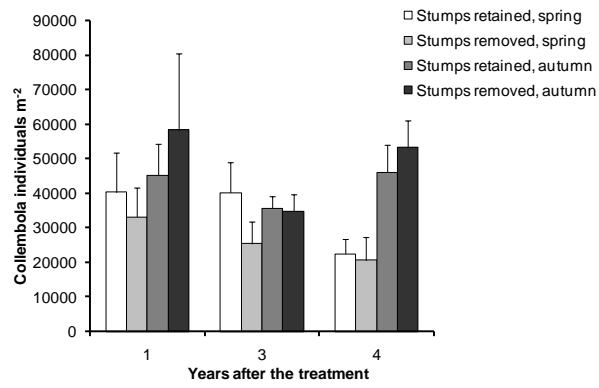


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576 Figure 1. Total numbers of enchytraeids (inds m⁻², mean + S.E.) in differently treated

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

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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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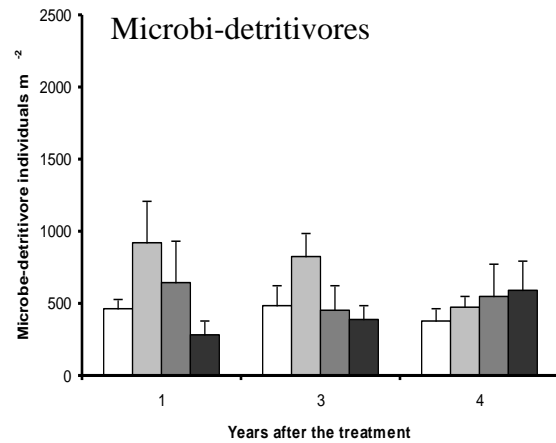
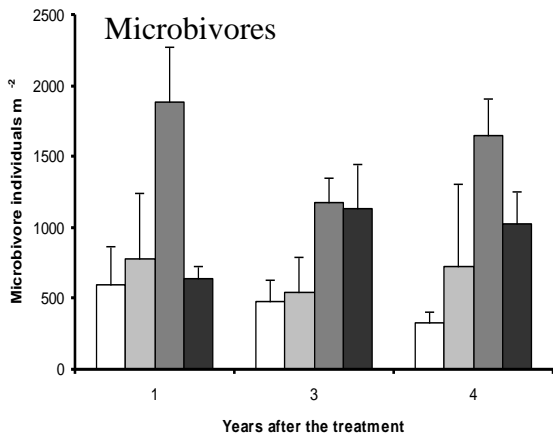
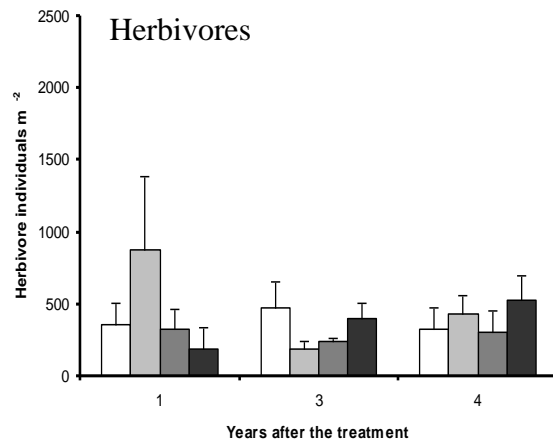
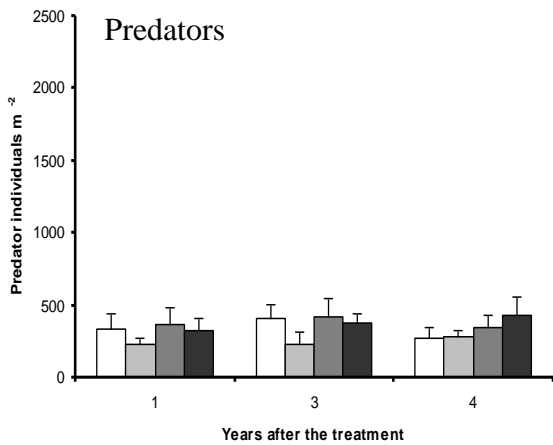
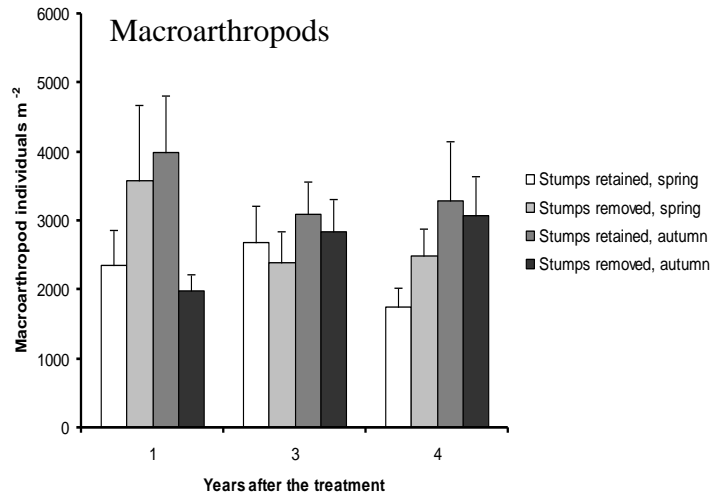
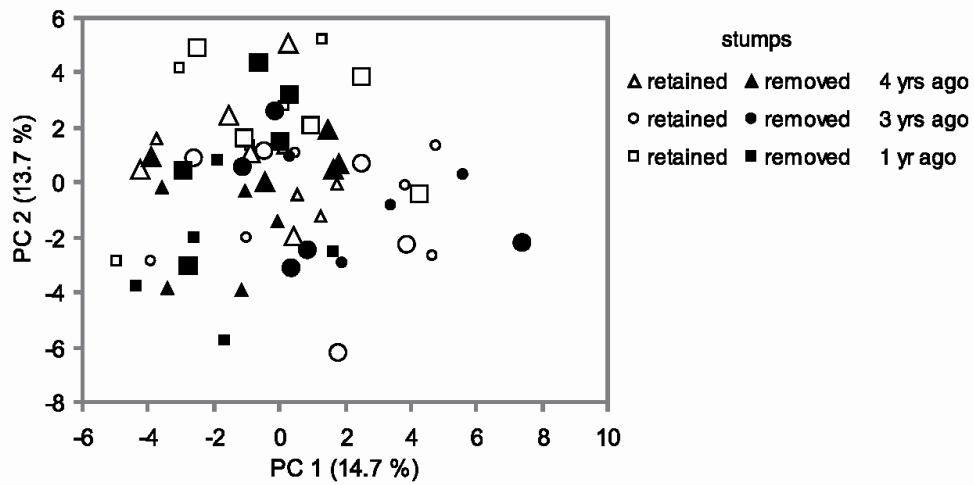


Figure 3. The numbers of macroarthropods in total, predators, herbivores, microbivores and microbi-detritivores (inds m^{-2} , mean + S.E.) in differently treated study sites one, three and four years after the treatment (n = 5).



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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.

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