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Green tree retention enhances negative short-term effects of clear-cutting on enchytraeid assemblages in a temperate forest

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Abstract

We studied the response of enchytraeid (Annelida: Oligochaeta) community structure to different forest management treatments via an open-field forestry experiment in a managed sessile oak-hornbeam forest in Hungary. The applied forestry treatments were 1) clear-cutting 2) clear

cutting with a small patch of retention tree group, 3) gap-cutting, 4) preparation cutting and 5) control (closed mature stand).

Our questions were: how did the selected forestry treatments influence the abundance and species richness of enchytraeids two years after the intervention, and how could the worms compensate the altered environmental conditions by vertical movements in topsoil layers (0–12 cm). The effects of the treatments on the species composition of the assemblages and species-specific responses were also analysed.

Two years after the treatments, a strong response of enchytraeids was observed in clear-cutting and even more in retention tree group: in both treatments the abundance and the species richness of enchytraeids were reduced. Species did not show vertical movements into deeper layers and were not able to tolerate the altered soil conditions caused by changed microclimate. Gap-cutting and preparation cutting did not differ significantly from control plots. Our study showed that right after the interventions tree retention at the size of one tree height in diameter had no sheltering effect on this important soil decomposer animal community. These results are in contrast with earlier findings in boreal zones, where soil organic layer is considered a well buffered habitat against environmental changes. Oppositely, enchytraeid assemblages in a temperate deciduous forest are more diverse but seem more vulnerable to management-related alterations in soil conditions (soil temperature increment, reduced soil moisture).

Keywords: potworms; soil invertebrates; mesofauna; vertical distribution; shelterwood forestry; forest management

1. Introduction

Compared to natural disturbances, forest management considerably changes the stand structure and tree species composition of the forests both at stand and landscape scales (Bengtsson et al., 2000, Lindenmayer and Franklin, 2002). Management modifies the biodiversity (including species richness, abundance structure, species composition) of many organism groups (Paillet et al., 2010, Chaudhary et al., 2016). It has many direct effects like eliminating important substrates and microhabitats (e.g. dead wood, cavity trees, rare admixing tree species, pits and mounds), that are essential for many organism groups such as bryophytes, lichens, fungi, saproxylic beetles and cavity nesting birds (Müller et al., 2007, Ódor et al., 2013). However, most organism groups are affected by the indirect effects of forest management via altered light, air and soil conditions (Suggitt et al., 2011, Tinya et al., 2009). Forestry can generate significant structural and chemical changes in forest soil (Thiffault et al., 2011, Kishchuk et al., 2014). These processes can alter soil invertebrate assemblages, which in turn influence ecosystem services like organic matter decomposition or nutrient cycling (Thomas and Packham, 2007, Zicsi et al., 2011).

Responses of soil mesofauna to forestry treatments were studied mostly in coniferous forests in boreal and mountainous regions, and were rather contrasting. A rapid increase in the number of soil springtails was observed 2–3 years after clear-cutting in Finland (Huhta, 1976), whereas Čuchta et al. (2012) reported a decline in numbers of edaphic collembolas after 3 years of clearing in the High Tatra National Park, Slovakia. Addison and Barber (1997) observed, that springtails were unaffected by clear-cutting in a mixed forest in Northern Ontario, as well as Siira-Pietikäinen et al. (2001), who did not find changes in the abundance and the community structure of collembolans as a result of forest harvesting. Mite populations responded with sharp decrease after clear-cutting (Huhta et al., 1969, Addison and Barber, 1997, Lindo and Visser, 2004). Lóšková et

al. (2013) found reduced oribatid abundance in those clearcuts, from which fallen timber had been removed. Tardigrades were more abundant in the deforested areas and seemed to be related to high soil moisture content (Uhía and Briones, 2002). These relationships were scarcely studied in temperate deciduous forests and such mesofauna members as enchytraeids.

Enchytraeid worms (Annelida: Clitellata) are small oligochaetes belonging to the soil mesofauna (Brussaard et al., 2012). Their ecological functions are similar to earthworms but at smaller scale (van Vliet et al., 1993, Didden and Marinissen, 1994). Enchytraeids are decomposers of decaying plant material but also known as microbivoreous and saprophagous organisms (Didden, 1993), hence, play an important role in nutrient cycling (Briones et al., 1998 a,b, Cole et al., 2000, Koutika et al., 2001). Their deposited excrements are microbial activity hotspots, consequently significant in mineralisation (Förster et al., 1995). Mixing of mineral and organic soil particles (van Vliet et al., 1995) indicate the indispensable role of this family of soil-dwelling invertebrates which have been easily considered as ecosystem engineers (Hastings et al., 2007, Pelosi and Römbke, 2016). Soil structure is affected by enchytraeids as their burrowing activity increases the soil porosity (Van Vliet et al., 1993) and through this, oxygen concentration and nutrient leaching potential of water-extractable compounds (Roithmeier and Pieper, 2009). Most of the enchytraeid populations (70–90%) are living in the uppermost 5–10 cm of the soil but some species can migrate to deeper layers depending on soil temperature (Dózsa-Farkas, 1992). Due to their high density in soil (Didden, 1993) Enchytraeids are also known as abundant decomposers in many habitats, such as forests.

Their sensitivity to forest management practices is known mainly from boreal forests, where the enchytraeid abundances increased due to forestry treatments (Huhta, 1976, Lundkvist, 1983, Siira-Pietikäinen et al., 2001, Malmström et al., 2009). However, all these boreal habitats were very poor

in enchytraeid species (one to six) and dominated (98–99%) by only one species, *Cognettia sphagnetorum*.

In this paper, we studied the effect of different forest management treatments on the community structure (abundance, species richness and species composition) of enchytraeid assemblages via an open-field forestry experiment. We compared forestry treatments that are widely used in temperate deciduous forests and belong to different forestry systems. Cutting areas with small patches of retention tree groups (or solitary retention trees) are common elements of forested landscape managed by clear-cutting (artificial regeneration) or shelterwood (natural regeneration) forestry systems (Matthews, 1991). The buffering effect of retention tree groups in clear-cuttings is widely studied for many organism groups with controversial statements (Rosenvald and Löhmus, 2008). Within shelterwood forestry system, the first step to the regeneration of forest stands is the preparation cutting (partial harvest) that accelerates natural tree regeneration before final cutting, which was also included in the experiment. In the last decades there was a paradigm shift in forest management from economically sustainable forestry to a more ecologically sustainable, multi-purpose forestry, which tries to mimic natural disturbances (Pommerening and Murphy, 2004, Bauhus et al., 2009). An important forestry practice regarding to this continuous cover forestry is the creation of gaps which was also included in this experiment.

In this study, the following questions were raised:

1. How do the selected forestry treatments influence the abundance and the species richness of enchytraeids in the topsoil (0–12 cm) two years after the intervention?
2. How can the individuals compensate the altered environmental conditions in the topsoil (0–12 cm) by vertical movements?
3. What are the effects of treatments on the species composition of the assemblages, and are there species specific responses on the treatments?

2. Materials and methods

2.1 Site description and experimental design

The study site was in the Pilis Mountains (47°40'N, 18°54'E) which is a north-eastern ridge of the Transdanubian Range, Hungary (Fig. 1A). The plots were situated on north-facing, moderate slopes (7.0–10.6°) at 380–450 m a.s.l. (Fig. 1B.). Average annual mean temperature is 9.0–9.5°C with a mean annual precipitation of 600–650 mm (Dövényi, 2010). The bedrock is limestone and sandstone with loess, the most common soil type is lessivage brown forest soil (luvisol in FAO soil classification), which is acidic (pH of the 0–20 cm layer is 4.6 ± 0.2 , Kovács et al., 2018). The site was situated in a managed sessile oak-hornbeam forest stand (Natura 2000 code: 91G0, European Commission, 1992). Due to the applied shelterwood system, the stand is even-aged (80 years old), and has relatively uniform structure and species composition. The upper canopy layer is dominated by sessile oak (*Quercus petraea* (Matt.) Liebl.), while turkey oak (*Quercus cerris* L.), European beech (*Fagus sylvatica* L.) and wild cherry (*Prunus avium* L.) also appeared as subordinate species. Secondary canopy layer was formed by hornbeam (*Carpinus betulus* L.) and manna ash (*Fraxinus ornus* L.) as subordinate species. The shrub layer is scarce. The understory layer is formed by general and mesic forest species, particularly hairy sedge (*Carex pilosa* Scopoli) and wood melic (*Melica uniflora* L.).

Four silvicultural treatments were carried out with control in a randomized complete block design, using six blocks as replicates. Treatments were as follows:

1. Control (C): closed-canopy stand without any treatment;
2. Clear-cutting (CC): a circular clear-cut (80 m in diameter, 0.5 ha), surrounded by closed stand;

3. Gap-cutting (G): an artificial circular gap in the closed stand (20 m in diameter, approximately one tree height/diameter ratio, 314 m²);
4. Preparation cutting (P): in a circle of 80 m diameter, 30% of the basal area of the dominant tree layer was felled spatially uniformly, and the complete secondary tree and shrub layer were also removed;
5. Retention tree group (R) within the clear-cut (CC) treatment: a circular group of retained dominant trees (20 m in diameter, 8-12 individuals).

The resulting number of plots was 30 (Fig. 1B,C).

Clear-cutting, retention tree group and preparation cutting represent characteristic stages of rotation forestry system, while gap-cutting is often implemented in the framework of continuous cover forestry (selection forestry) system. All experimental forestry treatments were established in December 2014 and January 2015.

The main aim of the general experiment was investigating the effect of these treatments on forest site environmental conditions (microclimate, soil conditions), biodiversity (including many organism groups) and stand regeneration. More information about the research is available on the website of the experiment (MTA Centre for Ecological Research, 2018).

Two years after the implementation (in 2016), considerable changes in the microclimate of the harvested plots were observed (Table 1. and Supplementary Material Table S1., for detailed analysis see Kovács et al., 2018).

2.2 Data collection

Data collection followed a Before-After Control-Impact design (Green, 1979): enchytraeid assemblages were surveyed in 2014 before any treatment and continuously after the implementations (in 2015 and 2016) applying the same methodology. Enchytraeids were collected

twice a year, in May and in September. Three soil samples per plot were taken with a split soil corer (diameter of 5 cm) to 12 cm depth (volume approximately 236 cm³ per sample). In 2015 and 2016 soil cores were vertically divided to three layers (0–4 cm, 4–8 cm and 8–12 cm, approximately 78 cm³ each in volume) to assess the vertical distribution of enchytraeids. Each sample was put separately in a plastic bag in the field, transferred to the laboratory and stored at 4 °C.

Samples from the same plot and layers were mixed and then a single aliquot with the volume of 78 cm³ was taken for worm extraction by wet funnel method (O'Connor, 1962).

Living enchytraeid individuals were kept in Petri-dishes with tap water, counted under dissecting microscope (Optika SZM-1, $\times 10 - \times 20$). They were identified *in vivo* under light microscope (Nikon Eclipse 50i, magnification between $\times 100 - \times 400$, mostly $\times 200$) using Schmelz (2003) and Schmelz and Collado (2010, 2012). Some specimens of each species were stored in 70% ethanol as a reference collection and deposited in the Institute for Ecology and Botany, MTA Centre for Ecological Research. For each species, the abundance per sample was counted. Density values (individuals per m²) were estimated by dividing the number of individuals per subsample by 0.0019625, which is the surface of the soil cores given in m². Juvenile specimens were not appropriate for identification, except for *Buchholzia appendiculata* (Buchholz, 1862), which were included when estimating total abundance.

2.3 Data analysis

Effect of the treatments as a fixed factor on the whole abundance and species richness of the topsoil (12 cm depth, 78 cm³ sample) was explored in each year (2014, 2015 and 2016) separately using general linear mixed models (GLMM; Faraway, 2006, Zuur et al., 2009). The reason of the separate analyses of the years is that they are qualitatively different (not simple time replications), 2014 represents before treatment, while 2015 and 2016 after treatment conditions. For abundance

Gaussian error structure and untransformed data, for species richness Poisson error structure and logarithmic link function were used, in each case blocks were defined as random factor. The treatment effect was analysed by F statistics for abundance and χ^2 statistics for species richness, likelihood ratio test based coefficient of determination of fixed factor (R^2) was also calculated (Barton, 2016). Tukey pairwise multiple comparisons of treatment levels were made using 0.05 significance level and general linear hypothesis tests (Hothorn et al., 2008).

Treatment effects on the abundance and species richness of different vertical layers in the surveys of 2015 and 2016 were analysed separately. In this case, treatment (five levels), vertical layers (three levels) and years (two levels) were used as fixed factors and blocks as random factor during the GLMM applying the same assumptions as above. All interaction terms of the fixed factors were included in the first model, which was selected by backward elimination based on log-likelihood ratio statistics (Faraway, 2006). Tukey-type multiple comparisons between treatment levels in each layer and year combination were based on least-squares means (Lenth, 2016). During the modelling, the normality as well as the homogeneity of the residuals were checked (Faraway, 2006).

The species composition of the treatments was explored by non-metric multidimensional scaling (NMDS) using Bray-Curtis distance function and square root transformation of the abundance data (Borcard et al., 2011). Separate analyses were run for each studied year. The separation of the treatments was also tested by permutational multivariate analysis of variance (PERMANOVA) using Bray-Curtis dissimilarity matrices (Andersson, 2001).

Associations of species with treatments in 2016 were evaluated by indicator species analysis (ISA), which is a combination of fidelity and specificity of the species to a certain treatment type (Dufrêne and Legendre, 1997). The indicator values of the species were tested via Monte-Carlo simulation using 1000 permutations, the accepted significance level was lower than 0.05.

All analyses were made in R version 3.4.1 (R Core Team, 2017). The GLMM of abundances were made by the "lme" function of "nlme" package (Pinheiro et al., 2017), that of species richness by "glmer" function of "lme4" package (Bates et al., 2015). Likelihood test based coefficient of determination was calculated by "r.squaredGLMM" function of "MuMIn" package (Barton, 2016). Multiple comparisons of linear hypothesis test were made by "glht" function of "multcomp" package (Hothorn et al., 2008) that of least-square means by "lsmeans" function of "lsmeans" package (Lenth, 2016). NMDS were made by "metaMDS" function, PERMANOVA by the "adonis" function of "vegan" package (Oksanen et al., 2017), and ISA by "indval" function of "abds" package (Roberts, 2013).

3. Results

3.1 Enchytraeid fauna and abundance

The total number of collected adult and subadult specimens (possessing sexual organs) was 2165 in 2014, 1431 in 2015 and 1397 in 2016 (Supplementary Material Table S2.). Remaining worms were juveniles which could be identified only to genus level. Their total number was 524 in 2014, 593 in 2015 and 483 in 2016.

35 enchytraeid species were found belonging to 7 genera during the whole period. The species richness of the whole sample was 35 in 2014, 32 in 2015 and 33 in 2016. 32 species occurred in all years, *Fridericia alata* Nielsen & Christensen, 1959, and *Fridericia conculcata* Dózsa-Farkas, 1986 only in 2014, *Fridericia regularis* Nielsen & Christensen, 1959 only in 2016. 24 species belonged to the genus *Fridericia* representing more than 50% of the total number of matured specimens each year. Both *Achaeta* and *Henlea* genera were represented by 3 species (*A. danica* Nielsen & Christensen, 1959, *A. eiseni* Vejdovský, 1878, *A. pannnonica* Graefe, 1989 and *H. nasuta* (Eisen, 1878), *H. perpusilla* Friend, 1911, *H. similis* Nielsen & Christensen, 1959).

Enchytronia and *Marionina* genera were only represented by one species (*En. parva* Nielsen & Christensen, 1959 and *M. communis* Nielsen & Christensen, 1959 respectively).

The abundance distribution of the species was skewed (Supplementary material Fig. S1). The number of common species (relative abundance higher than 5%) was 5 in 2014, and 7 both in 2015 and 2016. The number of rare species (relative abundance lower than 1%) decreased during the investigation, it was 18 in 2014, 12 in 2015 and 10 in 2016. Most prevalent species was *B. appendiculata* with a relative abundance of 12–20% (Supplementary material Fig. S1). Second dominant species was *F. connata* Bretscher, 1902 with 11–15% relative abundance. The frequency of other species varied with years and treatments. The relative abundance of *Henlea nasuta*, *H. perpusilla* and *H. similis* considerably increased between 2014 and 2016. Adversely, *Fridericia bisetosa* (Levinsen, 1884) and *F. bulboides* Nielsen & Christensen, 1959 decreased exceedingly in 2015 and disappeared completely in all treatments in 2016.

3.2 Treatment effects

3.2.1 Abundance and species richness

Before the establishment of the experiment, the enchytraeid abundance at the plots differed only marginally (the abundance was slightly higher in later clear-cut plots), while the species richness of the treatments was similar (Tab. 2, Fig. 2). After the establishment of the experimental harvests, the treatments had significant effects both on abundance and species richness. These effects were higher in 2016 than in 2015 (Tab. 2). The values of both variables were lower in clear-cutting and retention tree group treatment than in other treatments, in 2016 these values were even lower in retention tree group than in clear-cutting (Fig. 2).

3.2.2 Vertical distribution

Analysis of the effects of treatments, vertical layers and years had similar results for enchytraeid abundance and species richness (Tab. 3). In both cases, treatments and vertical layers had strong significant effects, while the effect of years was not significant. The only difference between them was that in the case of the abundance model the interaction terms were significant, while in species richness model they were not (except the treatment-year interaction). For both variables the values of clear-cutting and retention tree group were significantly lower than in other treatments in the 0–4 cm and 4–8 cm layers. In 8–12 cm layer only retention tree group treatment resulted significantly lower values (Fig. 3). It means that retention tree group treatment provided the most unfavourable conditions for enchytraeids, but clear-cutting had also a negative effect on the upper 8 cm of the soil. In these treatments all specimens disappeared from the upper soil layer and were also not recorded in deeper horizons since there was no accumulation of individuals in the lower layers. There were only few species found in retention tree group treatment: *Enchytraeus buchholzi* Vejdovský, 1879 in 0–4 cm layer, *F. connata* and *Fridericia rendsinata* Dózsa-Farkas, 1972 in 4–8 cm layer and *A. pannonica* in 8–12 cm layer. In the clear-cutting the following species could endure: *B. appendiculata* in 0–4 cm layer, *B. appendiculata*, *E. buchholzi*, *F. connata* and *H. nasuta* in 4–8 cm layer and *A. pannonica*, *E. buchholzi*, *F. connata*, *F. maculatiformis*, *F. sylvatica* Healy, 1979 and *H. nasuta* in 8–12 cm layer.

3.2.3 Assemblage composition

In 2014, prior to plot management, species composition at all plots regardless of the planned treatment on them was not significantly different based on PERMANOVA and on NMDS (Fig. 4). In the post-treatment period (in 2015 and 2016), the effects of the treatments were significant, and they were slightly stronger in 2015 than in 2016 (F value of PERMANOVA was 6.28 and

4.89, respectively). In 2015, the plots of control, preparation-cutting and gap-cutting had homogenous and separated groups, while the plots of retention tree group and clear-cutting were more heterogeneous but also separated (Fig. 4). In 2016 retention tree group was faunistically separated from other treatments. Control, gap-cutting and preparation cutting treatments created similar homogenous groups than in 2015, while clear-cutting intermingled with gap-cutting (Fig. 4).

According to the ISA, mainly control, gap-cutting and preparation cutting treatments were marked with associated species, the number was relatively higher in 2015 than in 2016 (Table 4). The same species were found in the control plots in the same two years (*Enchytraeus bulbosus*, *En. parva*, *F. bisetosa* and *F. isseli* Rota, 1994), which were extended by *F. paroniana* Issel, 1904 and *F. waldenstroemi* Rota & Healy, 1999 in 2015. *F. dura* (Eisen, 1879) and *H. perpusilla* were related to gap-cutting in both years, in 2015 they were complemented with *F. perrieri* (Vejdovský, 1878), *F. ratzeli* (Eisen, 1872) and *F. sylvatica*, while in 2016 *B. appendiculata* also preferred gap-cutting. In each year three species associated to preparation-cutting: *A. eiseni* in both years, while *A. danica* and *F. benti* Schmelz, 2002 in 2015 and *F. nemoralis* Nurminen, 1970 and *F. hegemon* (Vejdovský, 1878) in 2016. With the exception of *F. maculatiformis* Dózsa-Farkas, 1972 in 2015, no other species associated with clear-cutting and retention tree group treatments characterized by the lowest abundance and species richness of enchytraeids.

4. Discussion

Our results revealed that enchytraeids were sensitive to different forestry practices, especially to clear-cutting and retention tree group treatment. All measured variables (abundance, species richness and assemblage composition) decreased in these treatments. These changes are most likely to be explained by alteration of abiotic soil properties caused by these management practices.

The most drastic effect was observed in retention tree group where the soil moisture was the lowest. Here the drainage effect of the remaining trees along with the sun and wind arriving from the clear-cut can considerably desiccate the soil. The lower enchytraeid abundance in this treatment can be mainly explained by the mortality of the individuals since enchytraeids have low dispersion abilities. This explains why this invertebrate group is sensitive to any habitat alternation and responds immediately to changes. The results of their vertical distribution support this finding since worms did not migrate into deeper layer of soil but they disappeared. Coincidentally, in a Spanish pine forest (*Pinus pinaster* Aiton), with the exception of *C. sphagnetorum*, the remaining enchytraeid species did not show vertical migration to overcome adverse environmental conditions and, as a consequence of this, they were unable to tolerate the altered microclimate (Uhía and Briones, 2002). Although, some studies described soil as a relatively buffered environment (Setälä et al., 2000, Siira-Pietikäinen et al., 2001), our results suggest that in temperate zone forests this ascertainment can be true only for deeper soil layers.

In clear-cutting, a reduced abundance of worms was also found. However, the soil of clear-cutting areas can be significantly moister due to the lack of the trees, and because the forest understory responds to this management type with a strong enlargement of tree biomass and species richness (Collins et al., 1985, Jenkins and Parker, 2000) which can buffer the drying effect. Studies in boreal forests showed that the abundance of enchytraeids increased after a few years of clear-cutting (Huhta, 1976, Lundkvist, 1983, Siira-Pietikäinen et al., 2001, Malmström et al., 2009). This can be explained not only by the high amount of resources (i.e. felling residues, dying plant shoots and roots), but also by the increased radiation in clearings that lead to higher soil temperature. This can be advantageous in boreal forests where the average soil temperature is low. In contrast, Uhía and Briones (2002) recorded the minimum numbers of the dominant species *C. sphagnetorum* in late summer when temperature values were still high but the moisture content was low. Similarly, in

our experiment the high soil temperature and the drying force of the air which have a documented negative effect on the survival rate of enchytraeids (Springett, 1967, Springett et al., 1970, Abrahamsen, 1971, Briones et al., 1997) could prevail in clear-cutting in the first few years. The lack of leaf litter as a food source deficit indicator can also be a reason for low abundance in clear-cutting.

In temperate forests, gaps have the highest soil moisture as a result of the increased throughfall, the lack of tree transpiration and the shading effect of the surrounding stand (Gálhidy et al., 2006, Muscolo et al., 2014, Kovács et al., 2018). This could be a reason of the increased abundance of *Henlea* species, especially *H. perpusilla* (Table 4) which is considered as species often found in wet habitats (Schmelz and Collado, 2010). There were no significant differences according to control neither in abundance nor in species richness in preparation cutting, where dispersed arrangement of retained trees has a buffering effect on the forest site conditions and understory (Halpern et al., 2005, 2012, Zenner et al., 2012).

Earlier studies were mainly carried out in coniferous forests, where enchytraeids were dominated by only one species *C. sphagnetorum* (Nurminen, 1967, Lundkvist, 1983, Siira-Pietikäinen et al., 2001, Uhía and Briones, 2002, Malmström et al., 2009). This species – now considered a complex of species, see Martinsson et al. (2015) – had been classified as stress-tolerant species with asexual reproduction (fragmentation) (Graefe and Schmelz, 1999). Fragmentation is considered as a strategy in response to the environmental changes (Römbke, 1992, Pilipiuk, 1997, 2000), and is positively related to temperature (Standen, 1973). Fragmentation is also reported for *B. appendiculata* that was classified as an r-strategist species (Graefe and Schmelz, 1999) which could explain the dominance of this species in our clear-cut plots. However, enchytraeid assemblages in forest soils in the Pilis Mountains were much more complex without any single predominant species. Most of the species found are able to reproduce only sexually, thus, can be more sensible

to environmental changes. This might be a reason of decreasing number of rare species during the investigation.

5. Conclusions

Our results suggest that unlike reported earlier in previous studies (e.g.), the abundance and species richness of enchytraeids are negatively affected both by clear-cutting and retention tree group treatments. Such conclusion further supports the coordinated findings of two recent global meta-analyses (Mori and Kitagawa, 2014; Fedrowitz et al., 2014) which revealed that retention forestry in the temperate regions has a limited applicability as a tool of biodiversity conservation. Consequently, “lifeboating” capability determined by Gustafsson et al. (2010), as one of the most important functions of retention tree groups for soil macrofauna, is depending on the taxa, the spatial arrangement (dispersed vs. aggregated) and the extent of the retention groups (Siira-Pietikäinen and Haimi, 2009).

Based on our findings, the size of retained tree groups seems crucial, low buffering efficiency of such practice if the diameter of the remaining tree group does not exceed stand average height. Controversial short-term changes (*i.e.* 2–3 years) among boreal and temperate woodland habitats raise the question of the reliability of longer term predictions in temperate zone, albeit the response of enchytraeids may provide a good approximation for the trend of mesofauna. Long-term investigations (*i.e.* 10–12 years) in boreal forests found that the enchytraeid population had returned to the pre-treatment level of density (Huhta, 1976, Siira-Pietikäinen and Haimi, 2009). Based on our results it is difficult to predict their long-term response to environmental changes in temperate deciduous forests, since enchytraeid communities are much more heterogeneous here and seem more vulnerable. Therefore, continuing the systematic survey of this organism group is

crucial both for the more detailed exploration of their response to forestry and the more reliable projections of their community changes and the linked biogeochemical processes.

Moreover, in agreement with Uhía and Briones (2002) we can conclude that solely soil moisture and temperature are probably not sufficient to explain enchytraeid responses to environmental stress, therefore, further studies – long-term effects on the same site or involving other forests types – would be necessary to get a better understanding of the biological reactions to forest managements and their main drivers.

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Figure captions

Figure 1. (A) Map of the study area in the Pilis Mountains, Hungary; (B) Aerial photo of a block (©Viktor Tóth); (C) Experimental design of the study: six replicates as blocks and five treatments within each block.

Figure 2. Boxplot of abundance (individuals per m²) and species richness of enchytraeids in the treatments (X axis categories) and years (panels). Dots are the medians, boxes are interquartile ranges and whiskers are ranges without outliers. Abbreviation of the treatments are C – control, CC – clear-cutting, G – gap-cutting, P – preparation-cutting, and R – retention tree group. Significant differences based on multiple comparisons in different treatments within a year are marked by letters. Regarding to species richness, there was no significant treatment effect in 2014.

Figure 3. Boxplot of abundance (individuals per m²) and species richness of enchytraeids in years (panels), soil layers (subpanels) and treatments (x-axis categories). Dots are the medians, boxes are interquartile ranges and whiskers are ranges without outliers. Abbreviation of the treatments are C – control, CC – clear-cutting, G – gap-cutting, P – preparation-cutting, and R – retention tree group. Significant differences based on multiple comparisons in different treatments within a year and a vertical layer are marked by letters.

Figure 4. Non-metric multidimensional scaling ordination of the plots of different treatments based on the abundance of enchytraeids in different years. The plots are coloured by treatments: control – green, clear-cutting – red, gap-cutting – blue, preparation cutting – purple, retention tree group –

light brown. The compositional difference between treatments expressed as the results of the PERMANOVA (R^2 – coefficient of determination, F and p values) are portrayed on each panels.

Table 1. Changes of microclimate variables in the treatments two years after the implementation of the experiment (2016). For all variables, the values represent the mean within-block-differences from the control for the whole growing season (March–November). Measurement units: Photosynthetically active radiation ($\mu\text{mol m}^{-2}\text{s}^{-1}$); Relative diffuse light compared to open conditions (%); Air temperature ($^{\circ}\text{C}$); Relative humidity (%); Vapor pressure deficit (hPa) based on the variables air temperature and relative humidity indicating the drying capacity of the air; Soil temperature ($^{\circ}\text{C}$) at 1.5 cm below ground; Soil water content (m^3/m^3) measured at 10 cm below soil surface. The letters indicate the significant differences between treatment levels at $p<0.05$.

Variable	Clear-cutting	Gap-cutting	Preparation cutting	Retention tree group
Photosynthetically active radiation	665.7 ^a (± 339.4)	234.2 ^b (± 160.2)	131.7 ^c (± 85.4)	128.3 ^c (± 74.8)
Relative diffuse light	78.5 ^a (± 6.4)	32.4 ^b (± 6.4)	17.7 ^c (± 4.6)	14.3 ^c (± 9.2)
Air temperature	0.39 ^a (± 0.41)	0.17 ^{bc} (± 0.26)	0.11 ^b (± 0.18)	0.27 ^{ac} (± 0.24)
Relative humidity	-1.76 ^a (± 2.82)	0.06 ^b (± 2.42)	-0.27 ^b (± 1.82)	-1.93 ^a (± 1.78)
Vapor pressure deficit	0.609 ^a (± 0.643)	0.109 ^b (± 0.567)	0.114 ^b (± 0.376)	0.478 ^a (± 0.453)
Soil temperature	1.29 ^a (± 1.25)	0.47 ^b (± 0.88)	0.83 ^{bc} (± 0.60)	1.10 ^{ac} (± 0.76)
Soil water content	0.047 ^a (± 0.062)	0.089 ^b (± 0.077)	0.009 ^c (± 0.068)	-0.016 ^c (± 0.043)

Table 2. Treatment effect in general linear mixed models of abundance and species richness of enchytraeid assemblages. Treatment effect on abundance and species richness of enchytraeid assemblages derived from general linear mixed models. Gaussian error structure (F statistics) and Poisson error structure (Chi² statistics) were used for abundance and species richness respectively. Degrees of freedom were 4 for treatments and 20 for error. p: significance level; R²: likelihood-ratio test-based coefficient of determination of the models.

Variable	Year	F/Chi ² (df: 4; 20)	p	R ²
Abundance	2014	3.00	0.043	0.29
Abundance	2015	16.70	<0.001	0.76
Abundance	2016	50.17	<0.001	0.87
Species richness	2014	2.97	0.563	0.10
Species richness	2015	20.85	<0.001	0.44
Species richness	2016	60.38	<0.001	0.77

Table 3. Statistics of generalized linear mixed models for abundance (Gaussian error structure, F statistics) and species richness (Poisson error structure, Chi² statistics). Fixed factors were treatment (five levels), vertical layer (three levels) and year (two levels: 2015 and 2016). For abundance all interaction terms were included, likelihood-ratio test-based R² of the fixed terms was 0.68. The Treatment:Layer interaction was only included in the final model of species richness, likelihood-ratio test-based R² of the fixed terms was 0.62.

Variable	Abundance		
	F	df	p
Treatment	52.88	4	<0.001
Layer	35.61	2	<0.001
Year	2.21	1	0.139
Treatment:Layer	2.52	8	0.014
Treatment:Year	2.70	4	0.033
Layer:Year	9.70	2	0.001
Treatment:Layer:Year	2.92	8	0.005
Variable	Species richness		
	Chi ²	df	p
Treatment	104.52	4	<0.001
Layer	67.53	2	<0.001
Year	0.02	1	0.880
Treatment:Layer	13.77	8	0.078
Treatment:Year	18.24	4	<0.001
Layer:Year	1.60	2	0.449
Treatment:Layer:Year	5.22	8	0.737

Table 4. Indicator species analysis of enchytraeid species related to the treatments in 2015 and 2016. Only species significantly related to a treatment are listed (Monte Carlo simulation, $p < 0.05$, 1000 permutations). Numbers represent the mean abundance (mean individual m^{-2}) in different treatments: C – control, CC – clear-cutting, G – gap-cutting, P – preparation cutting, R – retention tree group. Treat.: treatments with the highest indicator values. Indval: indicator value related to the treatment, p: significance of the indicator value.

Species	C	CC	G	P	R	Treat.	Indval	p
2015								
<i>Enchytraeus bulbosus</i>	3.33	0.00	0.00	0.50	0.00	C	0.72	0.002
<i>Enchytronia parva</i>	6.83	0.00	0.83	4.67	0.33	C	0.54	0.003
<i>F. bisetosa</i>	5.00	0.33	0.00	0.17	0.83	C	0.79	0.001
<i>F. bulboides</i>	3.00	0.17	0.00	0.00	0.00	C	0.63	0.007
<i>F. isseli</i>	1.17	0.17	0.33	0.00	0.00	C	0.58	0.005
<i>F. paroniana</i>	6.00	0.50	0.17	0.00	0.00	C	0.90	0.001
<i>F. waldenstroemi</i>	2.50	0.00	1.17	0.00	0.50	C	0.50	0.008
<i>F. maculatiformis</i>	0.67	2.83	0.33	1.17	0.33	CC	0.65	0.001
<i>F. dura</i>	0.17	0.17	1.67	0.00	0.67	G	0.52	0.004
<i>F. perrieri</i>	0.33	0.00	4.17	0.67	0.00	G	0.81	0.001
<i>F. ratzeli</i>	0.00	0.00	0.83	0.00	0.00	G	0.50	0.022
<i>F. sylvatica</i>	1.84	5.50	6.50	2.67	2.17	G	0.35	0.044
<i>Henlea perpusilla</i>	0.00	0.00	2.83	1.33	0.33	G	0.63	0.004
<i>Achaeta danica</i>	1.33	0.83	0.33	5.83	0.67	P	0.65	0.003
<i>A. eiseni</i>	2.67	1.33	1.33	5.17	0.00	P	0.49	0.003
<i>F. benti</i>	0.00	0.00	0.00	2.50	0.83	P	0.62	0.003
2016								
<i>E. bulbosus</i>	2.00	0.00	0.00	0.00	0.00	C	0.67	0.006
<i>En. parva</i>	5.83	1.00	0.00	4.50	0.33	C	0.42	0.019
<i>F. bisetosa</i>	1.33	0.00	0.00	0.00	0.00	C	0.67	0.002
<i>F. bulboides</i>	2.00	0.00	0.00	0.00	0.00	C	0.50	0.038
<i>F. isseli</i>	3.00	0.67	0.33	0.67	0	C	0.54	0.015
<i>Buchholzia appendiculata</i>	11.17	6.67	14.67	3.00	0.00	G	0.41	0.008
<i>F. dura</i>	1.00	0.17	1.83	0.50	0.00	G	0.44	0.027
<i>H. perpusilla</i>	0.00	1.17	8.33	1.67	0.00	G	0.62	0.003
<i>A. eiseni</i>	0.83	0.17	0.50	3.67	0.67	P	0.52	0.011
<i>F. nemoralis</i>	3.33	3.33	1.50	5.83	0.33	P	0.41	0.017

<i>F. hegemon</i>	0.17	0.00	0.17	1.17	0.00	P	0.39	0.028
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Figure 1.

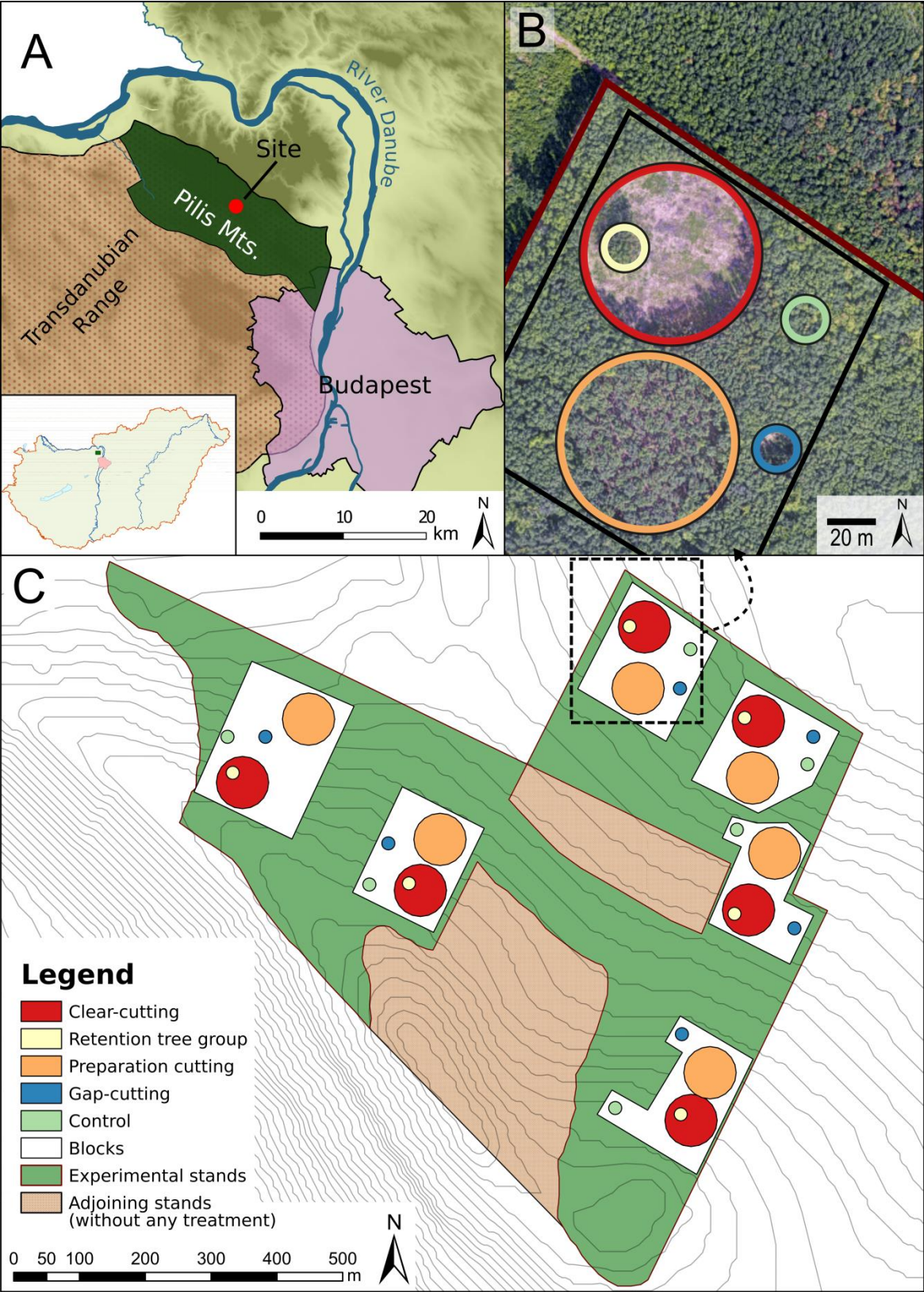


Figure 2.

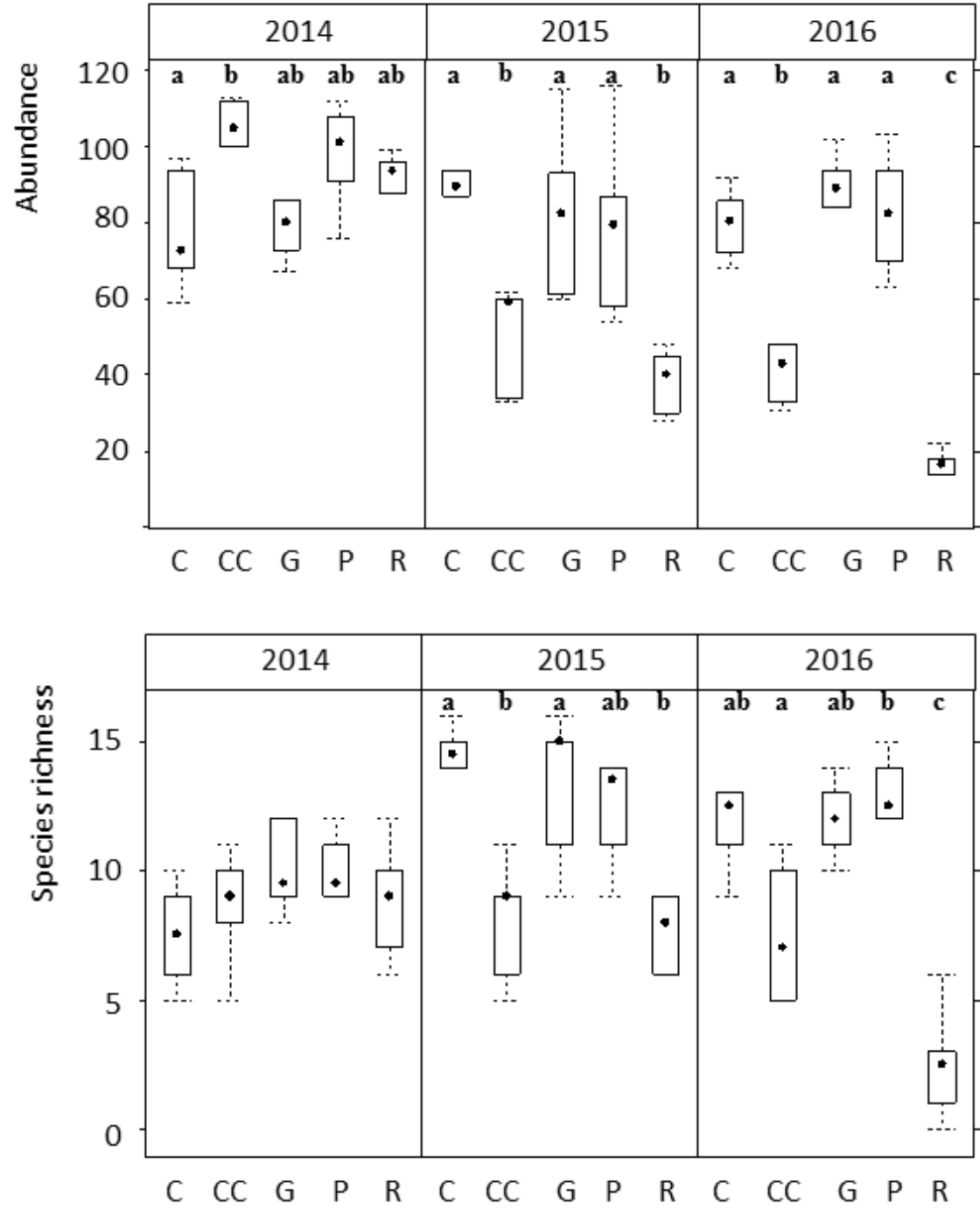


Figure 3.

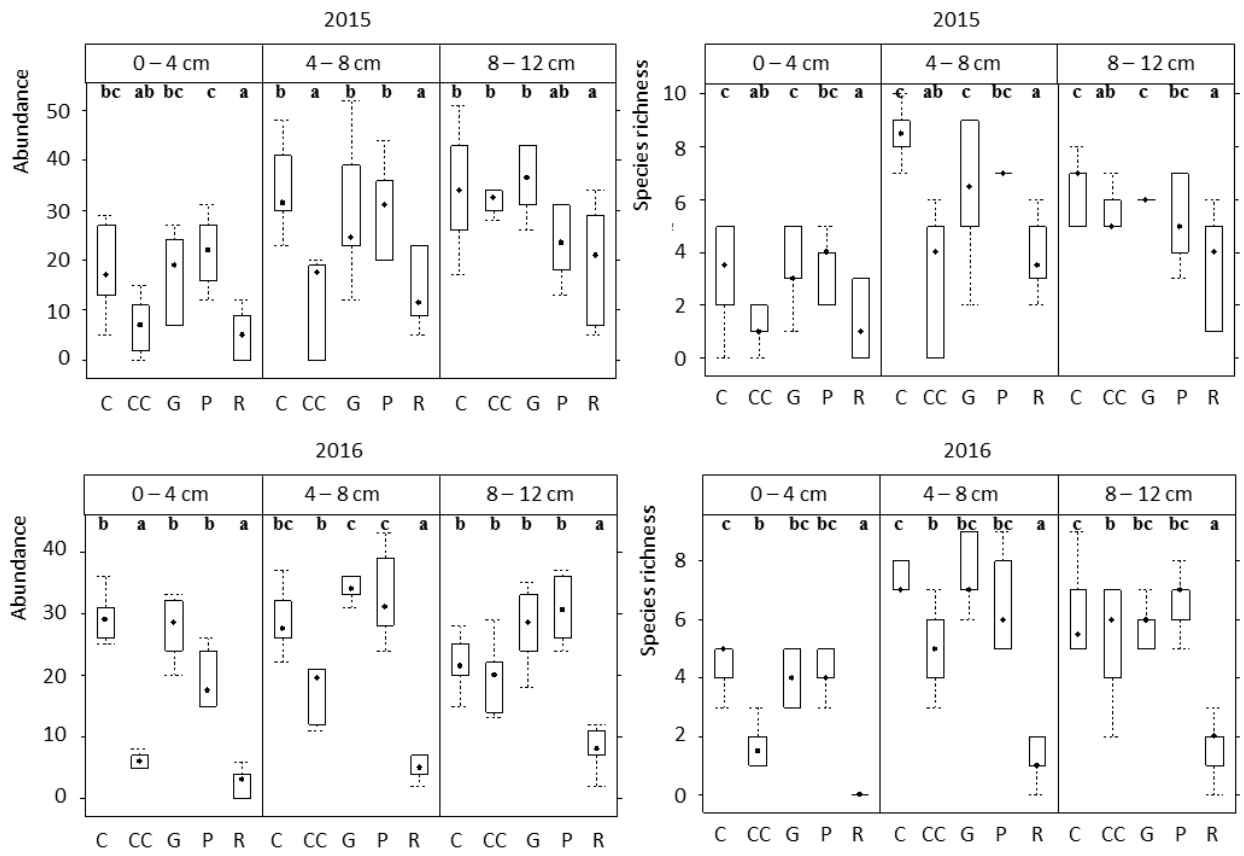
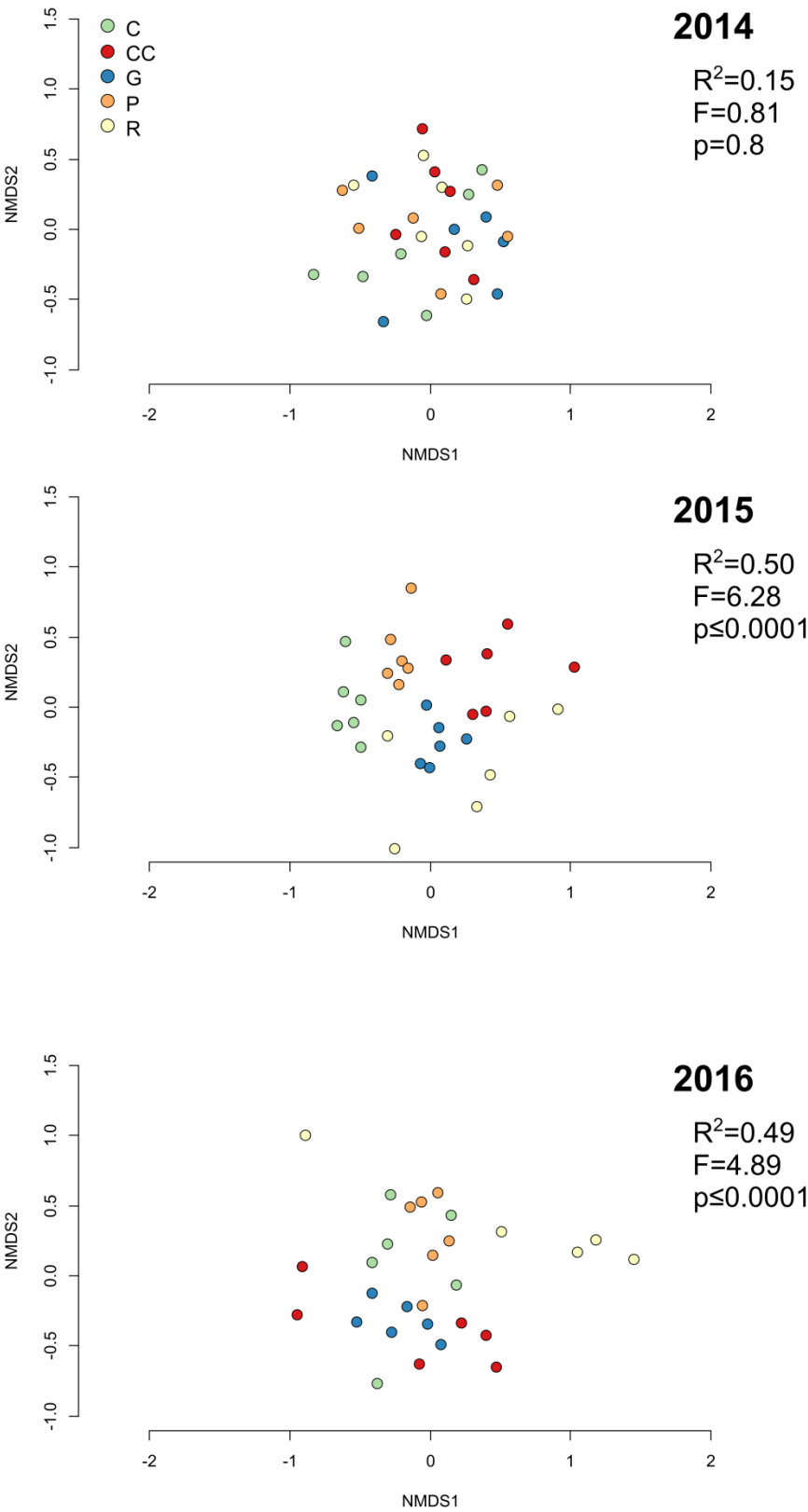


Figure 4.



Supplementary material

Table S1. Mean and standard deviations of the microclimate variables in Pilis Mountains, Hungary based on pooled 24-hour datasets collected in the growing season of 2016. Abbreviations of the variables: PAR: photosynthetically active radiation ($\mu\text{mol m}^{-2}\text{s}^{-1}$); DIFN: relative diffuse light compared to open conditions (%); T_{air}: air temperature (°C); RH: relative humidity (%); VPD: vapor pressure deficit (kPa) based on the variables T_{air} and RH indicating the drying capacity of the air; T_{soil}: soil temperature (°C) at 1.5 cm below ground; SWC: soil water content (m^3/m^3) measured at 10 cm below soil surface. In the case of PAR, daytime (6:00-18:00 UTC) means were calculated due to reasonability.

	Control		Clear-cutting		Gap-cutting		Preparation cutting		Retention tree group	
	<i>mean</i>	<i>SD</i>	<i>mean</i>	<i>SD</i>	<i>mean</i>	<i>SD</i>	<i>mean</i>	<i>SD</i>	<i>mean</i>	<i>SD</i>
PAR	47.890	75.507	707.215	318.417	279.053	159.874	177.722	110.927	175.096	104.377
DIFN	2.450	1.740	80.917	6.901	34.800	7.992	20.150	6.140	16.750	9.157
T_{air}	13.063	5.990	13.290	6.309	13.225	6.075	13.011	6.088	13.306	6.142
RH	76.709	10.521	75.093	9.970	76.893	10.536	76.626	10.107	75.098	10.077
VPD	0.403	0.243	0.465	0.263	0.413	0.253	0.409	0.240	0.444	0.249
T_{soil}	12.497	4.577	13.670	5.027	13.009	4.269	13.224	4.817	13.494	4.807
SWC	0.269	0.065	0.318	0.035	0.357	0.043	0.275	0.054	0.251	0.064

Table S2. List of species and their mean numbers with SD values found in the different treatments (C – control, CC – clear-cutting, G – gap-cutting, P – preparation-cutting, and R – retention tree group) in each year. Juvenile worms could only be identified only at genus level due to missing sexual organs. These specimens were excluded from species richness and species composition analysis, but they were reckoned in total abundance.

Species		Abbreviation	2014				
			C	CC	G	P	R
<i>Achaeta danica</i>	Nielsen & Christensen, 1959	<i>A_dan</i>	6±2.4	7±2.9	37±6.1	18±3.5	11±3.3
<i>A. eiseni</i>	Vejdovský, 1878	<i>A_eis</i>	0	21±4.2	35±5.2	7±2.9	0
<i>A. pannonica</i>	Graefe, 1989	<i>A_pan</i>	0	16±4.2	2±0.8	13±2.4	0
<i>Buchholzia appendiculata</i>	(Buchholz, 1862)	<i>B_app</i>	80±16.4	133±11.7	45±8.4	74±14.3	95±18.7
<i>Enchytraeus buchholzi</i> s.l.	Vejdovský, 1879	<i>E_buh</i>	56±8.8	72±6.2	40±7.8	62±15.5	66±12.5
<i>E. bulbosus</i>	Nielsen & Christensen, 1963	<i>E_bul</i>	7±2.9	0	5±2.0	27±5.1	6±2.4
<i>Enchytronia parva</i>	Nielsen & Christensen, 1959	<i>En_pa</i>	18±3.5	10±4.1	17±3.4	13±3.7	11±2.9
<i>Fridericia alata</i>	Nielsen & Christensen, 1959	<i>F_ala</i>	1±0.4	0	0	1±0.4	0
<i>F. cf. aurita</i>	Issel, 1905	<i>F_aur</i>	2±0.8	0	0	4±1.6	1±0.4
<i>F. benti</i>	Schmelz, 2002	<i>F_ben</i>	6±2.4	0	2±0.8	0	0
<i>F. bisetosa</i>	(Levinsen, 1884)	<i>F_bis</i>	19±4.0	13±3.5	25±5.1	3±1.2	12±3.1
<i>F. bulboides</i>	Nielsen & Christensen, 1959	<i>F_bul</i>	0	11±4.5	26±5.3	9±2.3	31±5.7
<i>F. cf. conculcata</i>	Dózsa-Farkas, 1986	<i>F_cul</i>	0	0	1±0.4	0	0
<i>F. connata</i>	Bretscher, 1902	<i>F_con</i>	69±9.6	60±7.0	47±5.8	76±7.7	76±6.7
<i>F. dura</i>	(Eisen, 1879)	<i>F_dur</i>	16±3.3	12±3.2	8±2.8	19±3.5	12±3.6
<i>F. galba</i>	(Hoffmeister, 1843)	<i>F_gal</i>	24±5.1	24±3.2	37±4.8	36±6.6	34±5.2

<i>F. glandifera</i>	Friend, 1911	<i>F_gla</i>	0	0	0	1±0.4	0
<i>F. hegemon</i>	(Vejdovský, 1878)	<i>F_heg</i>	0	3±1.2	0	0	0
<i>F. isseli</i>	Rota, 1994	<i>F_iss</i>	2±0.8	7±2.9	9±1.5	0	0
<i>F. lenta</i>	Schmelz, 2003	<i>F_len</i>	3±1.2	9±2.3	3±1.2	3±1.2	2±0.2
<i>F. maculatiformis</i>	Dózsa-Farkas, 1972	<i>F_maf</i>	0	1±0.4	4±1.6	10±2.0	5±1.2
<i>F. nemoralis</i>	Nurminen, 1970	<i>F_nem</i>	17±3.2	42±5.1	36±5.2	36±5.3	24±3.0
<i>F. paroniana</i>	Issel, 1904	<i>F_par</i>	4±1.0	5±2.0	11±2.9	2±0.5	1±0.4
<i>F. perrieri</i>	(Vejdovský, 1878)	<i>F_per</i>	2±0.5	0	2±0.8	11±3.0	0
<i>F. ratzeli</i>	(Eisen, 1872)	<i>F_rat</i>	0	1±0.4	10±2.7	0	3±1.2
<i>F. regularis</i>	Nielsen & Christensen, 1959	<i>F_reg</i>	0	0	0	0	0
<i>F. rendsinata</i>	Dózsa-Farkas, 1972	<i>F_ren</i>	13±4.0	1±0.4	0	4±1.6	0
<i>F. semisetosa</i>	Dózsa-Farkas, 1970	<i>F_sem</i>	0	0	0	4±1.2	4±1.2
<i>F. sylvatica</i>	Healy, 1979	<i>F_syl</i>	11±2.2	12±2.4	5±1.2	20±3.8	9±2.0
<i>F. tubulosa</i>	Dózsa-Farkas, 1972	<i>F_tub</i>	3±1.2	0	1±0.4	1±0.4	0
<i>F. waldenstroemi</i>	Rota & Healy, 1999	<i>F_wal</i>	0	2±0.8	3±1.2	4±1.2	2±0.8
<i>Henlea nasuta</i>	(Eisen, 1878)	<i>H_nas</i>	0	3±1.2	3±1.2	11±3.6	6±1.5
<i>H. perpusilla</i>	Friend, 1911	<i>H_per</i>	0	3±1.2	0	6±2.4	3±1.2
<i>H. similis</i>	Nielsen & Christensen, 1959	<i>H_sim</i>	3±1.2	3±1.2	0	7±2.9	6±1.7
<i>Marionina communis</i>	Nielsen & Christensen, 1959	<i>M_com</i>	3±1.2	0	3±1.2	0	9±3.7
<i>Achaeta</i> juv.		<i>A_juv</i>	13±3.5	12±2.5	19±2.0	12±2.2	4±1.6
<i>Enchytraeus</i> juv.		<i>E_juv</i>	51±6.1	64±7.2	18±4.4	55±7.6	74±5.5
<i>Fridericia</i> juv.		<i>F_juv</i>	32±2.3	53±3.2	38±3.6	38±2.9	32±3.9
<i>Henlea</i> juv.		<i>H_juv</i>	1±0.4	2±0.8	1±0.4	2±0.8	2±0.8
<i>Marionina</i> juv.		<i>M_juv</i>	1±0.4	0	0	0	0

Species		Abbreviation	2015				
			C	CC	G	P	R
<i>Achaeta danica</i>	Nielsen & Christensen, 1959	<i>A_dan</i>	8±2.8	5±2.0	2±0.8	35±2.9	4±1.2
<i>A. eiseni</i>	Vejdovský, 1878	<i>A_eis</i>	16±2.4	8±2.1	8±3.3	31±2.4	0
<i>A. pannonica</i>	Graefe, 1989	<i>A_pan</i>	12±2.5	7±2.0	8±1.5	6±2.0	15±1.6
<i>Buchholzia appendiculata</i>	(Buchholz, 1862)	<i>B_app</i>	55±3.2	32±4.4	61±4.2	26±7.0	0
<i>Enchytraeus buchholzi</i> s.l.	Vejdovský, 1879	<i>E_buh</i>	0	21±3.1	44±6.0	34±2.2	20±2.3
<i>E. bulbosus</i>	Nielsen & Christensen, 1963	<i>E_bul</i>	20±3.1	0	0	3±0.5	0
<i>Enchytronia parva</i>	Nielsen & Christensen, 1959	<i>En_pa</i>	41±2.8	0	5±2.0	28±2.3	2±0.8
<i>Fridericia alata</i>	Nielsen & Christensen, 1959	<i>F_ala</i>	0	0	0	0	0
<i>F. cf. aurita</i>	Issel, 1905	<i>F_aur</i>	7±1.2	0	0	6±0.6	1±0.4
<i>F. benti</i>	Schmelz, 2002	<i>F_ben</i>	0	0	0	15±2.2	5±1.6
<i>F. bisetosa</i>	(Levinsen, 1884)	<i>F_bis</i>	30±3.3	2±0.5	0	1±0.4	5±0.8
<i>F. bulboides</i>	Nielsen & Christensen, 1959	<i>F_bul</i>	18±3.0	1±0.4	0	0	0
<i>F. cf. conculcata</i>	Dózsa-Farkas, 1986	<i>F_cul</i>	0	0	0	0	0
<i>F. connata</i>	Bretscher, 1902	<i>F_con</i>	26±2.7	27±5.6	53±4.3	28±3.3	27±2.4
<i>F. dura</i>	(Eisen, 1879)	<i>F_dur</i>	1±0.4	1±0.4	10±1.2	0	4±0.8
<i>F. galba</i>	(Hoffmeister, 1843)	<i>F_gal</i>	34±3.1	4±1.6	22±1.8	32±4.0	6±1.7
<i>F. glandifera</i>	Friend, 1911	<i>F_gla</i>	0	0	0	1±0.4	0
<i>F. hegemon</i>	(Vejdovský, 1878)	<i>F_heg</i>	2±0.8	0	3±0.8	2±0.8	0
<i>F. isseli</i>	Rota, 1994	<i>F_iss</i>	7±0.8	1±0.4	2±0.5	0	0
<i>F. lenta</i>	Schmelz, 2003	<i>F_len</i>	1±0.4	1±0.4	6±0.9	8±2.4	6±2.4
<i>F. maculatiformis</i>	Dózsa-Farkas, 1972	<i>F_maf</i>	4±0.8	17±1.7	2±0.8	1±0.4	2±0.8
<i>F. nemoralis</i>	Nurminen, 1970	<i>F_nem</i>	42±3.7	21±3.1	21±3.0	45±5.9	8±2.2
<i>F. paroniana</i>	Issel, 1904	<i>F_par</i>	36±3.3	3±1.2	1±0.4	0	0

<i>F. perrieri</i>	(Vejdovský, 1878)	<i>F_per</i>	2±0.8	0	25±1.7	4±1.2	0
<i>F. ratzeli</i>	(Eisen, 1872)	<i>F_rat</i>	0	0	5±1.2	0	0
<i>F. regularis</i>	Nielsen & Christensen, 1959	<i>F_reg</i>	0	0	0	0	0
<i>F. rendsinata</i>	Dózsa-Farkas, 1972	<i>F_ren</i>	0	9±2.5	0	0	11±3.3
<i>F. semisetosa</i>	Dózsa-Farkas, 1970	<i>F_sem</i>	3±0.8	0	2±0.5	0	3±0.8
<i>F. sylvatica</i>	Healy, 1979	<i>F_syl</i>	11±3.0	33±3.6	39±2.6	16±2.0	13±3.1
<i>F. tubulosa</i>	Dózsa-Farkas, 1972	<i>F_tub</i>	0	0	4±1.6	0	0
<i>F. waldenstroemi</i>	Rota & Healy, 1999	<i>F_wal</i>	15±1.5	0	7±1.2	0	3±1.2
<i>Henlea nasuta</i>	(Eisen, 1878)	<i>H_nas</i>	0	8±1.9	3±1.2	4±1.6	0
<i>H. perpusilla</i>	Friend, 1911	<i>H_per</i>	0	0	17±2.3	8±2.4	2±0.8
<i>H. similis</i>	Nielsen & Christensen, 1959	<i>H_sim</i>	0	2±0.8	2±0.8	1±0.4	2±0.5
<i>Marionina communis</i>	Nielsen & Christensen, 1959	<i>M_com</i>	3±1.2	2±0.8	5±2.0	0	1±0.4
<i>Achaeta</i> juv.		<i>A_juv</i>	1±0.4	5±2.0	0	18±4.8	18±2.3
<i>Enchytraeus</i> juv.		<i>E_juv</i>	76±7.4	40±5.8	68±10.0	55±5.6	27±2.2
<i>Fridericia</i> juv.		<i>F_juv</i>	47±5.0	57±5.0	67±8.5	66±4.8	46±3.2
<i>Henlea</i> juv.		<i>H_juv</i>	0	0	2±0.5	0	0
<i>Marionina</i> juv.		<i>M_juv</i>	0	0	0	0	0

Species name		Abbreviation	2016				
			C	CC	G	P	R
<i>Achaeta danica</i>	Nielsen & Christensen, 1959	<i>A_dan</i>	14±2.9	2±0.8	0	13±2.1	4±1.2
<i>A. eiseni</i>	Vejdovský, 1878	<i>A_eis</i>	5±1.0	1±0.4	3±0.8	22±3.4	4±1.2
<i>A. pannonica</i>	Graefe, 1989	<i>A_pan</i>	0	3±1.2	10±2.0	4±1.0	13±2.0
<i>Buchholzia appendiculata</i>	(Buchholz, 1862)	<i>B_app</i>	67±6.6	40±4.3	88±2.1	18±7.3	0
<i>Enchytraeus buchholzi</i> s.l.	Vejdovský, 1879	<i>E_buh</i>	15±6.1	13±2.1	30±4.7	12±1.7	3±1.2
<i>E. bulbosus</i>	Nielsen & Christensen, 1963	<i>E_bul</i>	12±1.9	0	0	0	0
<i>Enchytronia parva</i>	Nielsen & Christensen, 1959	<i>En_pa</i>	35±3.9	6±1.7	0	27±2.1	2±0.8
<i>Fridericia alata</i>	Nielsen & Christensen, 1959	<i>F_ala</i>	0	0	0	0	0
<i>F. cf. aurita</i>	Issel, 1905	<i>F_aur</i>	1±0.4	0	0	1±0.4	0
<i>F. benti</i>	Schmelz, 2002	<i>F_ben</i>	0	0	0	7±2.0	0
<i>F. bisetosa</i>	(Levinsen, 1884)	<i>F_bis</i>	8±1.5	0	0	0	0
<i>F. bulboides</i>	Nielsen & Christensen, 1959	<i>F_bul</i>	12±3.1	0	0	0	0
<i>F. cf. conculcata</i>	Dózsa-Farkas, 1986	<i>F_cul</i>	0	0	0	0	0
<i>F. connata</i>	Bretscher, 1902	<i>F_con</i>	48±6.8	17±3.4	43±4.5	51±4.8	1±0.4
<i>F. dura</i>	(Eisen, 1879)	<i>F_dur</i>	6±1.5	1±0.4	11±1.5	3±0.8	0
<i>F. galba</i>	(Hoffmeister, 1843)	<i>F_gal</i>	51±5.2	0	54±7.0	51±3.1	0
<i>F. glandifera</i>	Friend, 1911	<i>F_gla</i>	0	0	0	7±2.9	0
<i>F. hegemon</i>	(Vejdovský, 1878)	<i>F_heg</i>	1±0.4	0	1±0.4	7±1.3	0
<i>F. isseli</i>	Rota, 1994	<i>F_iss</i>	18±3.6	4±1.6	2±0.8	4±0.8	0
<i>F. lenta</i>	Schmelz, 2003	<i>F_len</i>	6±2.0	0	2±0.8	10±2.7	0
<i>F. maculatiformis</i>	Dózsa-Farkas, 1972	<i>F_maf</i>	0	6±1.3	2±0.8	0	0
<i>F. nemoralis</i>	Nurminen, 1970	<i>F_nem</i>	20±3.8	20±2.8	9±2.1	35±2.6	2±0.8
<i>F. paroniana</i>	Issel, 1904	<i>F_par</i>	1±0.4	0	7±1.8	0	0

<i>F. perrieri</i>	(Vejdovský, 1878)	<i>F_per</i>	14±4.8	0	5±1.2	8±2.8	0
<i>F. ratzeli</i>	(Eisen, 1872)	<i>F_rat</i>	4±1.2	4±1.6	7±1.6	1±0.4	0
<i>F. regularis</i>	Nielsen & Christensen, 1959	<i>F_reg</i>	0	0	15±3.2	6±2.0	0
<i>F. rendsinata</i>	Dózsa-Farkas, 1972	<i>F_ren</i>	2±0.8	7±1.8	0	6±2.4	1±0.4
<i>F. semisetosa</i>	Dózsa-Farkas, 1970	<i>F_sem</i>	3±0.8	0	0	0	0
<i>F. sylvatica</i>	Healy, 1979	<i>F_syl</i>	16±3.7	3±0.5	10±1.6	23±2.1	1±0.4
<i>F. tubulosa</i>	Dózsa-Farkas, 1972	<i>F_tub</i>	1±0.4	3±1.2	6±2.4	13±2.7	1±0.4
<i>F. waldenstroemi</i>	Rota & Healy, 1999	<i>F_wal</i>	7±1.9	0	8±1.5	1±0.4	0
<i>Henlea nasuta</i>	(Eisen, 1878)	<i>H_nas</i>	4±1.6	32±6.3	28±10.0	8±1.5	0
<i>H. perpusilla</i>	Friend, 1911	<i>H_per</i>	0	7±1.8	50±5.8	10±2.7	0
<i>H. similis</i>	Nielsen & Christensen, 1959	<i>H_sim</i>	0	14±4.4	10±2.3	6±2.4	0
<i>Marionina communis</i>	Nielsen & Christensen, 1959	<i>M_com</i>	9±3.2	21±3.0	19±4.7	7±1.8	0
<i>Achaeta</i> juv.		<i>A_juv</i>	11±2.2	0	1±0.4	9±2.8	31±1.9
<i>Enchytraeus</i> juv.		<i>E_juv</i>	28±4.1	14±3.0	30±4.6	44±5.6	13±2.6
<i>Fridericia</i> juv.		<i>F_juv</i>	53±5.7	52±5.9	91±8.0	81±6.4	18±2.1
<i>Henlea</i> juv.		<i>H_juv</i>	0	0	0	0	0
<i>Marionina</i> juv.		<i>M_juv</i>	7±2.9	0	0	0	0

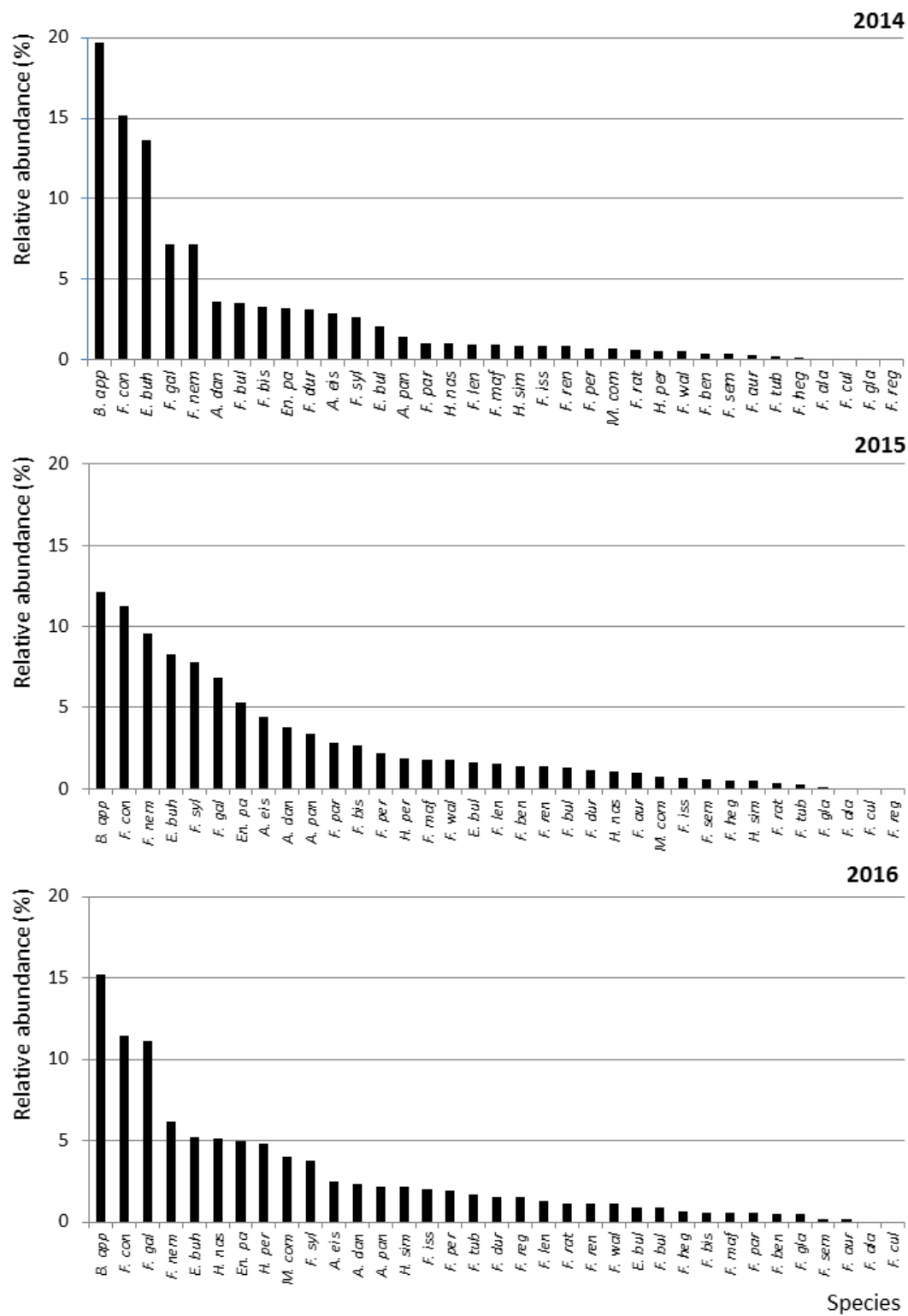


Figure S1. Distribution of relative abundance (%) of the found species in 2014, 2015 and 2016. Species name abbreviations are shown in Table S2.