



Collembola communities and soil conditions in forest plantations established in an intensively managed agricultural area

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Abstract The challenges of a changing climate have directed greater attention to afforestation, but the effects of afforestation on soil fertility and soil biota have not been fully clarified. To explore changes in the soil conditions in two 20-year-old forest plantations established in formerly intensively fertilized plots of agricultural land, we focused on the current developmental state of the sites that received the most fertilizer and evaluated soil properties and Collembola (springtails) communities. Sessile oak (*Quercus petraea*) and black locust (*Robinia pseudoacacia*) that had been planted in the afforestation sites were assessed for differences between plantations of native and invasive species. Five adjacent reference associations, including forests and open habitats, were also analyzed and compared. Results showed that the soils in the two afforested sites were similar in their properties and Collembola communities to those of the control cultivated forests, but differed from each other

in pH, calcium, phosphorus, and ammonium content. The available potassium and phosphorus contents in the soil of the sessile oak plantation were still high, while the soil organic matter content was adequate (SOM > 2.0%) in both plantations. Species richness of Collembola ranged from 18 in the cultivated arable land to 43 in the relict forest. Only a few species typical for forests (e.g., *Neanura muscorum*, *Isotomiella minor*, *Entomobrya muscorum*) were detected in the young plantations, while species characteristic of open habitats (e.g., *Protaphorura campata*, *Lepidocyrtus cyaneus*) occurred as well. Although more individuals and species of Collembola were present in the soil of young plantations than in arable fields, their community diversities were significantly lower compared to the control forest stands. Collembola community diversity differed significantly also between the two plantation types (with native and non-native tree species). Mean abundance in the afforested sites was about 2.5 times higher than in the cultivated arable land, yet far lower than the mean abundance in the control forests.

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Introduction

The most optimistic scenarios limit the global mean temperature increase to 1.5 °C relative to the pre-industrial level until the end of the twenty-first century, but only if the increase in atmospheric CO₂ concentrations can be efficiently moderated (Rogelj et al. 2012, 2018). Land-use strategies must be thoroughly reconsidered to meet this goal. Forests continue to play a crucial role in the global carbon cycle (Bouwman and Leemans 1995; Lal 2004; Bonan 2008; Luysaert et al. 2008; Pan et al. 2011; Law et al. 2018).

Consequently, afforestation can make an important contribution to mitigate the effects of changing climate (Canadell and Raupach 2008; Mackey et al. 2013; Lawson and Michler 2014) and provide corridors within forest biomes, increase biodiversity, protect against soil erosion, regulate the hydrologic cycle, mitigate the effect of radiation and contribute to carbon, oxygen and nutrient cycling (Lindenmayer and Hobbs 2004; Farley et al. 2005; Arneith et al. 2010; Huang et al. 2010; Pawson et al. 2013; Peng et al. 2014; Paul et al. 2016; Torralba et al. 2016). The environmental benefits of afforestation are structural and functional, which depend on spatial design and maturity (Cunningham et al. 2015). While forests in many regions have been cleared and converted to agricultural uses (Gibbs et al. 2010; Laurance et al. 2014), abandoned or low-quality agricultural lands are more.

Arable land comprises 46.58% of Hungary's total area (KSH 2019). Agricultural activities have led to large-scale habitat conversions during the past century (Demeny and Centeri 2008; Munteanu et al. 2014; Konkoly-Gyúró and Balázs 2016). With the increase in cultivated areas, the area of forests and grasslands decreased significantly in Hungary. At present, more than half of the country is under agricultural cultivation. In the nineteenth century, grasslands in Hungary covered 30% of the area; the proportion now is only 8.5% (KSH 2019). Concerning forests, the proportion of forested areas in Hungary was only 11.8% after the First World War, although an estimated 85.5% of the country's current area should be naturally forested (Bartha 2000). These marked changes in the vegetation cover have led to habitat loss, fragmentation, and a complex set of biotic responses in the soil environment including significant loss of biodiversity (Poschlod et al. 2005; Heiniger et al. 2014). Nevertheless, over the past few decades, a considerable proportion of agricultural land in Europe has been converted into different land-use types such as grasslands or forests (Jongman 2002; Cunningham et al. 2015). A subsequent national afforestation program has increased forest cover in Hungary to 21%, and the forest cover continues to increase. In many cases, however, afforestation has occurred with non-native species including black locust (*Robinia pseudoacacia*), which occupies one-fourth of the forested area in Hungary today (KSH 2019). Afforestation of abandoned or low-quality agricultural land has increased worldwide during the last two decades; thus, the ability to predict the long-term effect on soil property and biota following land-use change has become essential.

Afforestation can induce alterations in soil carbon content and pH (e.g., Paul et al. 2002; Vesterdal et al. 2002; Chen et al. 2008; Berthrong et al. 2009; Varamesh et al. 2014; Cunningham et al. 2015; Gao et al. 2018) and greatly affect the redistribution of soil macronutrients into biomass, nutrient cycling and stocks in soils (Farley and Kelly 2004; Shaifullah et al. 2009; Deng et al. 2017). Since soil biota are essential for

soil processes and functions, they are widely used as bioindicators to monitor soil conditions after land-use changes (e.g., Kladvik 2001; Sousa et al. 2006; Vanbergen et al. 2007; Zhao et al. 2013; Menta et al. 2018). Characteristic communities of soil biota can call attention to properties of their natural environment that might be difficult to quantify as a measure of physical or chemical factors or vegetation type (Hopkin 1997). Springtails (Collembola) are among the best indicators within the soil mesofauna. They provide an important contribution in the mineralization of organic matter (Bardgett and Chan 1999; Kaneda and Kaneko 2008), thus helping plants absorb nutrients. Quick alterations in their community characteristics due to any type of soil degradation or changes in land-use make them suitable as test organisms as well (Giller et al. 1997; Zepelini et al. 2009; Paul et al. 2011). However, responses after afforestation have not been completely ascertained. According to the heterogeneity theory, the diversity of animal communities is driven by habitat heterogeneity (Tews et al. 2003). We hypothesized that afforestation of highly degraded land provides higher heterogeneity over time, which is also reflected in Collembola diversity. Mosaics of surrounding habitats and corridors also play crucial role in colonization of newly afforested sites as source of fauna and dispersal routes (Sousa et al. 2004). This study presents the results of soil analyses and investigations of Collembola communities in two former long-term fertilization experimental sites afforested with native sessile oak (*Quercus petraea*) and non-native black locust, with adjacent characteristic habitats used as controls. Cultivated arable field was surveyed to get an idea of the initial community conditions, while the grassland formed on abandoned arable land represents the first phase of succession. Forests of both tree species that were managed for a long time, and a relict association were also included in the studies to obtain a more accurate comparative picture of the soil biological status of the studied plantations.

The main objectives were to (1) assess the soil conditions of the experimental sites 20 years after afforestation by comparing them to the control habitats; (2) evaluate the Collembola community response to the conversion of arable land to different types of forest plantation; (3) explore whether Collembola communities to some extent indicate traces of previous land-use; (4) specify the soil variables that are driving and determining Collembola communities after the conversion to forest has been made; and (5) detect the changes in community composition and biodiversity pattern along this habitat gradient.

Materials and methods

Study area

The study area is located in the Gödöllő Hills near Budapest in central Hungary (Fig. 1). The slightly sloping land

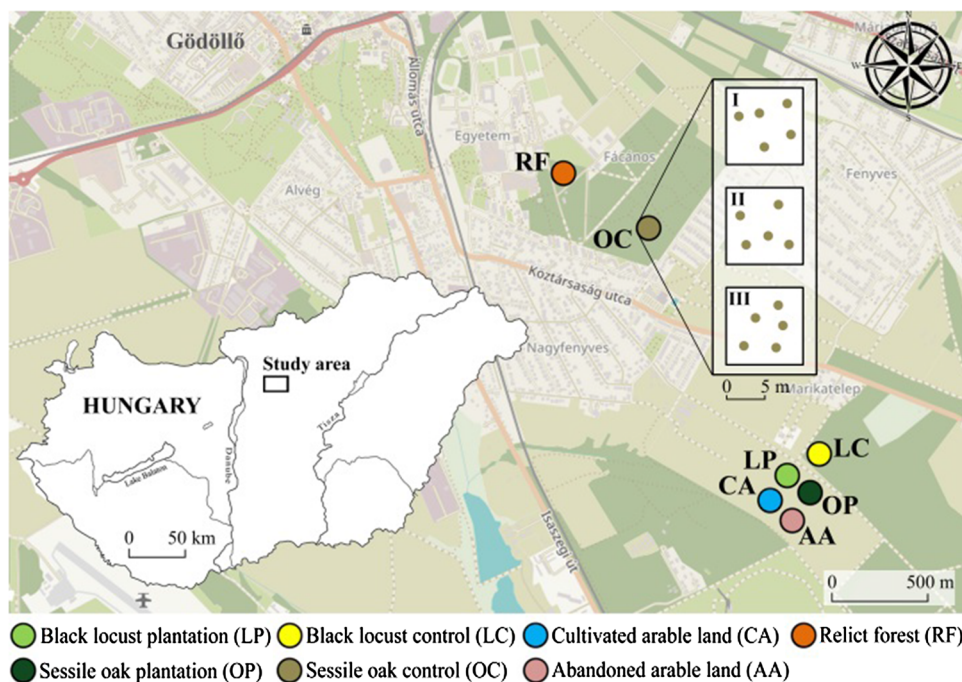
stands between the flat area of the Great Hungarian Plain and the mountain range of northern Hungary. An approximately equal amount of intensive agricultural lands and cultivated forests characterize the landscape. The most commonly grown crops are grains, while the forests consist of native oak-dominated associations, as well as planted forests consisting of invasive species dominated by black locust. The natural vegetation also contains open and closed grasslands. Climatic conditions are moderately cold, moderately dry continental, with average yearly mean temperatures of 9.5–9.7 °C. The minimum temperature is –16 °C and the maximum is 33 °C. Annual hours of sunlight amounts to 1950 h while annual precipitation is 540–580 mm. It is a rather dry area, and the available groundwater volume is low (Dövényi 2010).

The two examined 20-year-old plantations had been used for long-term fertilization experiments before the afforestation with sessile oak (OP), a common native species, and black locust (LP), a fast-growing, non-native species. The average 60–90 cm-thick soil of the study area was formed on bedrock sand mixed with loess from the Tertiary. The topsoil is shallow with an average 35-cm-thick humus layer. Carbonate appears at an average depth of 60 cm, while the groundwater is below 4 m. This soil can be classified as Luvic Endocalcic Phaeozem (Loamic, Aric) (IUSS Working Group WRB 2014). Originally, the upper 20 cm had a sandy soil texture that was slightly acidic pH (pH_{KCl} 5.0), had low SOM content (1.3–1.5%), low available phosphorus ($p = 15 \text{ mg kg}^{-1}$) and moderate potassium ($K = 107 \text{ mg kg}^{-1}$) content and weak water-holding capacity. Until the afforestation, soil NO_3^- , p and K was abundant as a consequence

of NPK fertilization, while the Ca and Mg concentration as well as organic matter content and pH were low (Füleky and Debreczeni 1991; Füleky and Kovács 1993). Plots treated with the highest amount of fertilizer were investigated in the current research because the most pronounced changes occurred as a result of high fertilizer doses, as outlined in a previous examination (Harta et al. 2018).

To characterize the current developmental state of these two ca. 20-year-old forest plantations (LP, OP), we assigned five control sites to represent the adjacent cultivated (CA) and abandoned arable lands (AA), managed sessile oak (OC) and black locust (LC) forests, and an old-growth relict forest (RF). The structure of the black locust plantation (LP) is relatively open, with tree density of 2200 trees ha^{-1} and canopy closure of approximately 50%. The shrub layer is patchy (40–50% cover), while the herb layer covers a minimum of 30% of the site and was dominated by the grass *Bromus sterilis*. The sessile oak plantation (OP) is more closed, with tree density of 3000 trees ha^{-1} and canopy closure of 80–90%. The shrub layer is less developed (20% cover), and only a few herbaceous species appear in the sparse herb layer. Most of the characteristics of the managed 38-year-old control black locust forest (LC) are similar to those of the plantation; canopy closure is 45–50%, and tree density is 1500 trees ha^{-1} . The shrub layer cover is about 50%, while the herb layer is dense, with a coverage of 60–70%. The managed control oak forest (OC) is a two-storey stand, with tree density of 900 trees ha^{-1} and canopy closure of 90%. Both shrub (50%) and herb layers (60%) are well developed. The old-growth forest (RF) is a relict association of *Aceri campestris–Quercetum petraeae-roboris*) endemic in this

Fig. 1 Map showing location of study area in Gödöllő, Central Hungary. Coloured circles represent the studied habitats (sites). Insert shows the size of replicates I–III with five random sampling plots set up within each site



landscape. The two-layered forest stand has fairly well-developed, species-rich shrub and herb layers.

Soil sampling and analysis

After litter removal, soil samples were taken from the top 20 cm layer in September 2017. Each test site was represented by three replications (10 m × 10 m plots), where one replication consisted of five randomly collected (Fig. 1) and then thoroughly mixed soil cores (ca. 50 g). Samples were air-dried, crushed, and sieved through a 2.0-mm grid. To compare our results to the results in older studies, we used the same analytical methods as described by Füleky and Debreczeni (1991) and Füleky and Kovács (1993). The pH was determined in distilled water ($\text{pH}_{\text{H}_2\text{O}}$) and in KCl-suspension (pH_{KCl}) as well, in a ratio of 1:2.5 using a potentiometric method. Soil organic matter (SOM) content was determined by the Tyurin (1931) method (wet oxidation by $\text{K}_2\text{Cr}_2\text{O}_7$ and H_2SO_4). Mineral nitrogen ($\text{NO}_3^- + \text{NH}_4^+$) forms were defined by Parnas-Wagner distillation using potassium-chloride (1% KCl). Soluble phosphorus (AL-P) and potassium (AL-K) contents were extracted using ammonium-lactate-acetic acid and Ca and Mg contents with 1 M KCl solution (MSZ 20135 1999). Calcium carbonate (CaCO_3) content was measured with the Scheibler method according to the volume of released CO_2 after diluted hydrochloric acid (10% HCl) was added to the sample (Allison and Moodie 1965). The plasticity index according to Arany (K_A) was defined as well, which is the amount of distilled water (expressed in dm^3) contained in 100 g air-dried soil at the upper limit of plasticity (Buzás 1993). This method is also appropriate to gain information on the water-holding capacity of the sampled soil.

Sampling and extraction of Collembola

Corresponding to the sampling design for determining soil properties (Fig. 1), five nondestructive soil samples of 100 cm^3 were taken at a 10-cm depth in each selected plot using a soil corer with a 3.6-cm diameter. Mesofauna was extracted within 14 days from the soil samples into 70% ethanol at room temperature using unheated Berlese-Tullgren funnels. Collembola individuals were counted and identified to the species level (adult and young individuals except for those at the first instar stage). Taxonomic classification was primarily based on the checklist of Hungarian fauna (Dányi and Traser 2008).

Due to the uncertainties of species identity of *Pseudosinella wahlgreni* (see Stomp 1971), the *Pseudosinella* species with 5 + 5 ocelli found in the control oak forests has been listed as *Pseudosinella* sp. *wahlgreni*-group based on the main morphological characters.

Data analyses

Habitat soil variables were tested for normality (Shapiro–Wilk test) and homogeneity of variances (Levene's test), then tested with a one-way ANOVA to test for differences among the seven studied sites. Significance level was set at $p < 0.05$. Prior to this, the independence of cases was provided by collecting samples randomly. If Levene's test was significant ($p < 0.05$), the unequal variance (Welch F test) version of ANOVA was used. Significant differences between the groups were evaluated by Tukey's pairwise post hoc test (Copenhaver and Holland 1988). If the required assumptions were strongly violated (normality test $p < 0.05$), the nonparametric Kruskal–Wallis test was used (allowed rate $p < 0.05$) with Dunn's pairwise post hoc test instead (raw p values) (Dunn 1964).

Collembolan abundance was calculated as the number of individuals per square meter (ind. m^{-2}). Two measures of diversity were computed: the Shannon index (Shannon and Weaver 1949); and Pielou's evenness index (Pielou 1966), respectively. To compare Shannon diversities, the Hutcheson t test was used (Hutcheson 1970). Renyi diversity profiles, incorporating further diversity measures (e.g., species richness, Simpson index) apart from the Shannon index, were constructed to rank Collembola communities according to diversity (Tóthmérész 1997). A community of higher diversity is characterized by a profile that runs consistently higher than the profile of a less diverse community. The degree of dominance was expressed with McNaughton's dominance index (CDI) calculated as the percentage of abundance contributed by the two most abundant species (McNaughton 1967).

Principal coordinate analysis (PCoA) was performed to order the Collembola communities in the different habitat types (Legendre and Legendre 2012). The distance matrix calculated for PCoA was determined using the Bray–Curtis dissimilarity measure (Bray and Curtis 1957).

To explore potential relationships between Collembolan species composition and soil variables, a direct ordination method, canonical correspondence analysis (CCA) was applied with forward variable selection. To conduct the analysis, we used species abundance for the main matrix, while the environmental matrix included the variables pH, SOM, mineral N, AL-P and AL-K. Species in less than 5 samples or represented by fewer than 10 specimens were not entered in the analysis to avoid misrepresentation of the sampling data. In parallel, an unrestricted Monte Carlo test was performed by considering 1000 random permutations to reveal the effect of the constraining variables used in the analysis. Statistical analyses were carried out using the software Past ver. 3.17 (Hammer et al. 2001) and CANOCO ver. 4.5 (ter Braak and Šmilauer 2002).

Results

Collembola communities

In total, 11,410 specimens from 15 families, 40 genera, and 76 species were sampled and identified (Supplementary Table S1) at the seven study sites in the Gödöllő Hills. The greatest species richness was found in samples of the relict oak stand, while the lowest species richness was observed in the cultivated field (Table 1). Both the oak and black locust forest plantations supported higher species richness, and Shannon diversities were significantly higher when compared to the cultivated site ($t = 16.843$ and 9.534 , respectively, $p < 0.001$). Nevertheless, when compared to the control forest habitats, significantly lower diversity was observed in both plantations ($t = 5.33$ – 38.63 , $p < 0.001$). Marked difference was also found between the two plantation types ($t = 10.65$, $p < 0.001$), where the soil of the native oak plantation supported a more diverse community. Renyi diversity profiles emphasized the same pattern (Fig. 2).

Apart from high species richness and diversity in the abandoned arable land, it had the most even community structure, which was also supported by the highest equitability (J) and a relatively low mean community dominance index (CDI) value. Regarding abundance, we found significant difference among habitats (Kruskal–Wallis, $H = 18.84$, $p < 0.05$), and the difference between the cultivated arable field and young afforested habitat was more pronounced, averaging 2.5 times higher in the young plantations. Considering different types of forest plantations, although mean abundance was higher in the black locust plantation, a significant difference could not be observed (Dunn’s, NS). Mean abundance was the highest in the old relict oak forest.

The PCoA ordination performed on the plot-to-plot dissimilarity matrix clearly separated the communities of the open habitats from those of the plantations and control forests (Fig. 3). Regarding the forest communities, there was a certain degree of overlap between the oak and black locust

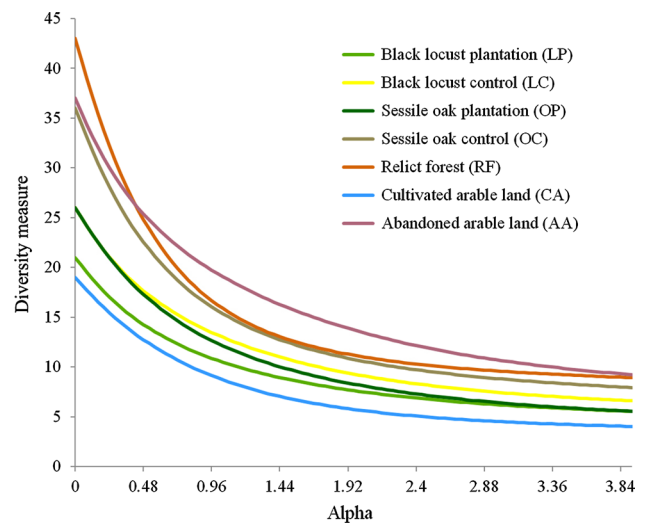


Fig. 2 Diversity profiles of the Collembolan communities. The profiles incorporate the exponential of the Rényi index, which indicates the total species richness for $\alpha = 0$, an index proportional to the Shannon diversity for $\alpha = 1$ and the logarithm of the reciprocal Simpson diversity for $\alpha = 2$, respectively

plantations and between the managed control forests. The community of the old-growth relict forest showed a clear separation.

The result of the canonical correspondence analysis (CCA) provides more detailed information on species-habitat relationship (Fig. 4). The eigenvalue was significant for both axis 1 (0.427) and axis 2 (0.169), and the explained variance of both axes were also relatively high (61.71% and 17.92%, respectively). The Monte Carlo permutation test confirmed the significance of both axis 1 and axis 2 ($p < 0.01$ and $p < 0.05$, respectively). From the variables entered into the analysis, axis 1 mainly represents soil pH, soluble phosphorus (AL-P), soil organic matter content (SOM), and plasticity (K_A), while axis 2 mostly represents mineral nitrogen ($\text{NO}_3^- + \text{NH}_4^+$) and soluble potassium content (AL-K).

Table 1 Mean abundance (\pm SE) and site based community indices of Collembola (A: abundance (ind. m^{-2}); S: species richness; H' : Shannon diversity index; J : Pielou’s evenness index; CDI: community dominance index)

Indices	Reforested sites		Control forests		Agricultural lands		
	OP	LP	OC	LC	RF	CA	AA
A	6 067 \pm 320 ab	6 433 \pm 254 abc	14 040 \pm 711 cd	11 780 \pm 476 bcd	23 033 \pm 1 185 d	2 633 \pm 279 a	12 033 \pm 1 095 bcd
S	26	21	36	26	43	18	37
H'	2.516	2.368	2.752	2.582	2.788	2.188	2.965
J	0.772	0.778	0.768	0.793	0.741	0.743	0.821
CDI	39.67	41.97	33.76	37.75	28.74	53.16	29.81

In the case of abundance, bold letters (a, b, c and d) indicate significantly different groups after Dunn’s test ($p < 0.05$). The same letter indicates that they belong to the same group. For sampling site abbreviations, see the legend of Fig. 1

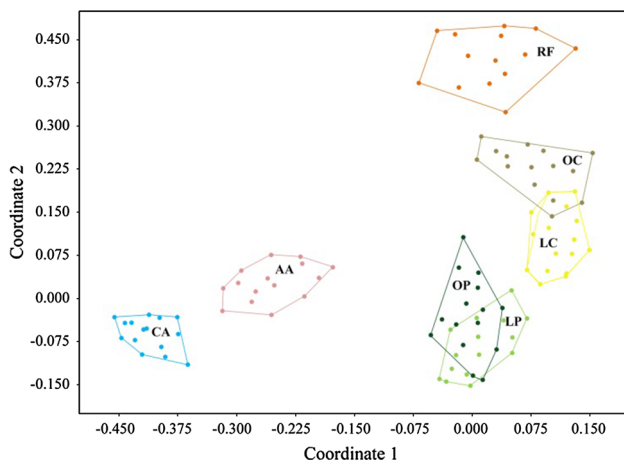


Fig. 3 Principal coordinate analysis ordination of Collembola communities from the forest plantations and control habitats using Bray–Curtis distances. For sampling site abbreviations, see the legend of Fig. 1

Along the gradient of axis 1, a clear habitat sequence can be observed from the open arable fields, through the young plantations toward the old relict forest. Along axis 2, the cultivated arable field exhibited a remarkable separation.

Collembola species characteristic for open habitats (e.g., *Ceratophysella succinea*, *Lepidocyrtus paradoxus*, *Isotoma caerulea*) are distributed toward the positive side of axis 1, while species collected principally or exclusively in forests (e.g., *Neanura muscorum*, *Entomobrya muscorum*, *Pseudosinella horaki*) are ordinated on the negative side of the same axis. As shown by their ordination on the negative side of axis 2, species like *Brachystomella parvula* or *Folsomides parvulus* are also well adapted to unfavorable soil conditions (low organic matter content, higher fertilizer load) and are grouped near the cultivated arable field plots.

Soil habitat condition

Based on the measured soil variables, the studied habitats were characterized as sandy textured soils, with relatively acidic or neutral pH and lack of carbonates. Nevertheless, they had remarkable differences for most of the variables (Table 2). Soil plasticity (K_A) values differed significantly

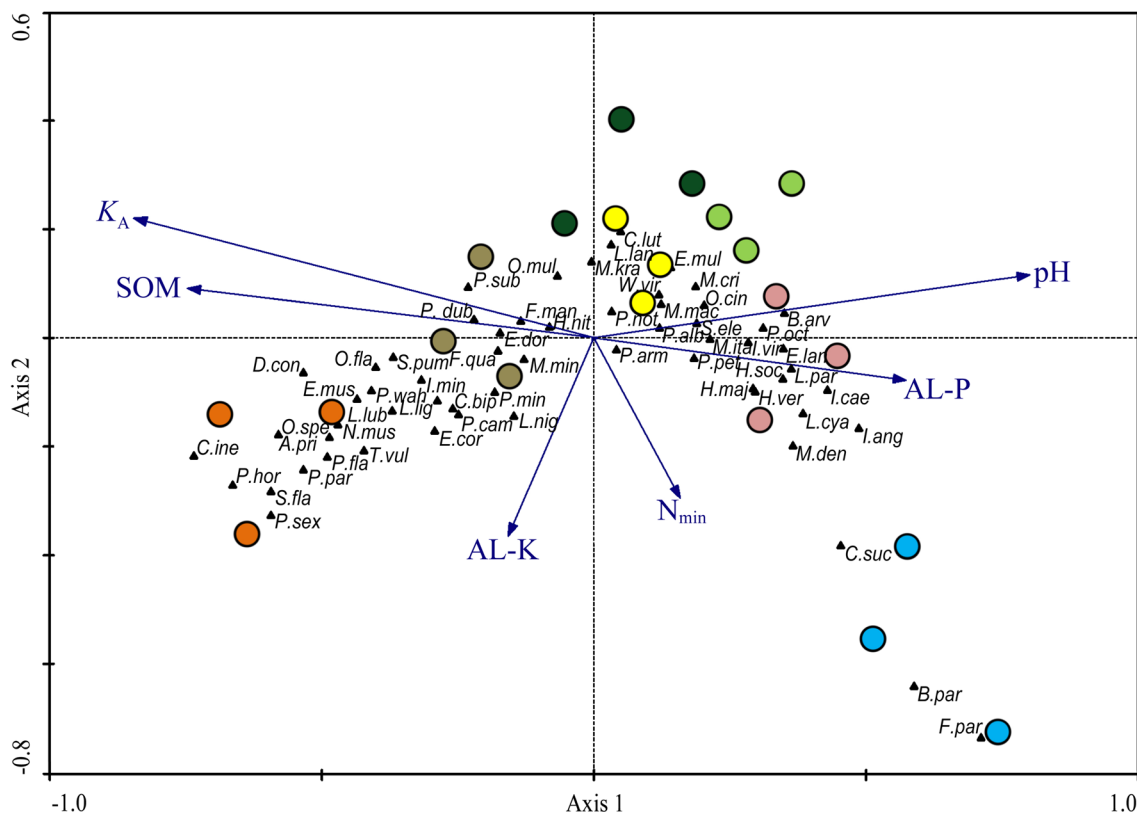


Fig. 4 Ordination biplot of canonical correspondence analysis with mean abundances of Collembola species and selected soil variables (SOM, soil organic matter content; K_A , plasticity index according to Arany; soil pH; $N_{\min} = \text{NO}_3^- + \text{NH}_4^+$, mineral nitrogen; AL-P, solu-

ble phosphorus; AL-K, soluble potassium. For sampling site symbols (coloured circles), see Fig. 1. Collembola species abbreviations consist of the initial letter of the genus name, followed by the first three letters of the species name

among habitats (Kruskal–Wallis, $H = 18.18$, $p < 0.01$). The highest values occurred in the RF and the lowest in the CA. Significant differences in soil organic matter (SOM) content were also observed among habitats (Kruskal–Wallis, $H = 16.63$, $p < 0.01$). As expected, the highest SOM content was found in the soil of the old-growth relict forest (RF), showing significant difference (Dunn’s, $p < 0.001$) from the cultivated land (CA). Nevertheless, the afforested sites (OP, LP) did not significantly differ from the control forests (Dunn’s, NS). The pH_{H_2O} values were $0.5 < pH$ unit higher than those of pH_{KCl} in all habitats, indicating residual acidity. Significant differences were observed in both pH_{H_2O} (ANOVA, $F = 19.50$, $p < 0.01$) and pH_{KCl} (ANOVA, $F = 54.53$, $p < 0.001$). The most acidic soil was associated with the old-growth relict forest (RF), while the highest pH occurred in the abandoned arable land (AA). Both types of pH values were also low in the sessile oak plantation, while the pH values in black locust plantation were similar to the open habitats (CA, AA) and the managed black locust control forest (Tukey’s HSD test, NS). Significant differences were observed among habitats also in macronutrient contents, such as phosphorus (ANOVA, $F = 14.89$, $p < 0.001$), potassium (ANOVA, $F = 7.82$, $p < 0.001$) and mineral nitrogen (ANOVA, $F = 4.61$, $p < 0.01$).

Discussion

Our results for soil properties and Collembola community species composition, diversity, and abundance suggest that the studied forest plantations can be ranked as transitions

among the cultivated arable field and the control forests. As the results of PCoA based on the Bray–Curtis dissimilarity (Fig. 3) revealed, the open control habitats (CA, AA) showed consistent separation from the forest plantations (OP, LP) and forest control habitats (OC, LC, RF). Destructive agricultural management practices, such as tillage, use of fertilizers and pesticides, alter soil structure and chemical properties leading to soil degradation, thereby negatively affecting the habitat of soil microarthropods, including Collembola (Cortet et al. 2002; Brussaard et al. 2007; Kalia and Gosal 2011; Wachira et al. 2014; Tsiafouli et al. 2015). Cultivation often causes organic carbon loss in soils (Collins et al. 2000; Song et al. 2005), which is demonstrated in the lowest SOM content in the studied cultivated agricultural land (CA). The low SOM content is coupled with low soil plasticity (K_A) values, indicating poor water retention ability and resulting dry conditions in this sandy soil. A high concentration of available phosphorus, caused by fertilization and facilitated decomposition due to tillage, was also expected (Lupwayi et al. 2007). The aforementioned practices and their implications on soil condition generally tend to reduce Collembola diversity (Frampton 1997; Giller et al. 1997; Alvarez et al. 2001; Gruss and Twardowski 2012; Twardowski et al. 2016). Decreased abundance and species richness are characteristic for arable habitats, as reported in several regions (e.g., Kováč and Miklisová 1997; Culik et al. 2002; Sousa et al. 2006; Vanbergen et al. 2007; Muturi et al. 2009). Thus, as expected, the lowest Collembola species richness, diversity, and abundance was found in the cultivated site (CA). Besides the mentioned alteration caused by agricultural practices, arable soils are also considered

Table 2 Measured soil variables (mean ± SD) in afforested sites and control habitats. K_A : plasticity index according to Arany, SOM: soil organic matter, $CaCO_3$: calcium-carbonate content, N min: $NO_3^- + NH_4^+$; mineral nitrogen content

Variable	Reforested sites		Control forests			Agricultural lands	
	OP	LP	OC	LC	RF	CA	AA
K_A^*	27 ± 1.0 ab	28 ± 1.5 ab	32 ± 1.0 bc	27 ± 0.58 ab	44 ± 4.2 c	21 ± 0.58 a	33 ± 2.1 bc
SOM (%) [*]	2.11 ± 0.28 bc	2.22 ± 0.20 bc	2.01 ± 0.22 ab	1.46 ± 0.34 ab	3.97 ± 1.60 c	0.83 ± 0.27 a	2.19 ± 0.04 bc
pH H_2O	5.57 ± 0.43 b	6.85 ± 0.12 d	5.86 ± 0.32 bc	6.68 ± 0.52 cd	4.56 ± 0.32 a	6.27 ± 0.04 bcd	7.07 ± 0.34 d
pH KCl	4.56 ± 0.59 ab	6.26 ± 0.13 de	4.95 ± 0.40 bc	6.05 ± 0.74 cde	3.63 ± 0.16 a	5.21 ± 0.09 bcd	6.48 ± 0.41 e
$CaCO_3$ (%)	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	1.83 ± 3.16	0.00 ± 0.00	0.00 ± 0.00	0.85 ± 1.48
Ca (mg kg^{-1}) [*]	265 ± 86 a	671 ± 16 b	456 ± 27 ab	1452 ± 1797 ab	323 ± 145 a	431 ± 13 ab	1878 ± 2220 b
Mg (mg kg^{-1})	91.6 ± 17.5 abc	101.7 ± 10.5 bc	119.3 ± 12.2 c	74.6 ± 7.4 ab	87.1 ± 12.2 ab	99.1 ± 5.4 abc	68.5 ± 10.9 a
AL-P (mg kg^{-1})	122 ± 6 c	20 ± 13 a	12 ± 10 a	38 ± 7 ab	30 ± 10 ab	44 ± 9 ab	75 ± 39 bc
AL-K (mg kg^{-1})	224 ± 36 cd	156 ± 16 abc	105 ± 34 a	121 ± 1 ab	248 ± 33 d	202 ± 32 bcd	181 ± 52 abcd
NH_4-N (mg kg^{-1})	10.1 ± 3.9 b	1.3 ± 0.70 a	6.7 ± 3.8 ab	3.6 ± 1.9 ab	5.5 ± 3.6 ab	3.4 ± 1.3 ab	2.7 ± 0.72 a
NO_3-N (mg kg^{-1})	2.8 ± 1.6 a	7.7 ± 7.5 a	4.3 ± 2.5 a	5.5 ± 2.2 a	29.6 ± 15.1 b	2.9 ± 0.69 a	5.5 ± 1.9 a
N min (mg kg^{-1})	12.8 ± 4.6 ab	9.0 ± 7.3 a	10.9 ± 5.7 a	9.0 ± 1.7 a	35.1 ± 18.2 b	6.3 ± 0.67 a	8.2 ± 2.6 a

Bold letters (a, b and c) indicate significantly different groups after Tukey’s or Dunn’s test ($p < 0.05$). In the case of each parameter, the same letter indicates that they belong to the same group. If there is no letter, it means no significant difference was observed. Asterisk (*) indicate those comparisons made with Kruskal–Wallis test. For sampling site abbreviations see the legend of Fig. 1

to be poor in resources, mainly due to the lack of abundant vegetation (plant residues, roots). Nevertheless, some species can also use alternative food resources like bacteria or fungi (Lagerlöf and Andrén 1991; Hiol et al. 1994). In the arable soil samples, several cosmopolitan species were collected (e.g., *Brachystomella parvula*, *Ceratophysella succinea*, *Mesaphorura macrochaeta*, *Parisotoma notabilis*, *Entomobrya multifasciata*, *Folsomides parvulus*, *Lepidocyrtus cyaneus*), which are often found in intensively managed arable soils (Kováč and Miklisová 1997; Filser et al. 2002; Debeljak et al. 2007; Twardowski et al. 2016) and are reportedly showing tolerance to unfavorable conditions (e.g., drought, low SOM content, high concentration of fertilizer components such as nitrogen or phosphorus) as suggested by the CCA ordination (Fig. 4).

The release from environmental stress associated with the agricultural practices will lead to a marked response of biomass (Chauvat et al. 2007). After a transition to grassland, the values of SOM can rapidly increase (McLauchlan et al. 2006; Liu et al. 2020), as the abandoned agricultural land (AA) has more than twofold SOM content compared to the cultivated one. It is associated with improved water-holding ability indicated by the higher value of plasticity. Under these changed conditions, the colonization rate is usually high, and the Collembola population often shows a rapid increase (Kaczmarek and Kajak 1997; Chauvat et al. 2007). The spontaneous successive ruderal vegetation in the abandoned arable site (AA) provided habitat for more abundant communities and also led to increased species diversity. The value of Shannon diversity even exceeded that of the relic forest (RF). Nevertheless, the intersection observed between the Rényi diversity profiles of the sampled old-growth forest and grassland on the abandoned site (Fig. 2) emphasizes that open and forest areas supports different Collembola communities that are not comparable based solely on diversity (Tóthmérész, 1997). Apart from the ubiquitous species already present in the cultivated site, further species (*Hypogastrura vernalis*, *Entomobrya lanuginosa*, *Lepidocyrtus paradoxus*, *Isotoma viridis*) characteristic for open ecosystems such as grasslands (Ponge 1993; Ponge et al. 2003; Chauvat et al. 2007) were detected which, however, have specific ecological requirements including denser vegetation cover or higher SOM content.

The abandonment of farmlands offers large areas suitable for afforestation (Young et al. 2005), and this option has also been used in our study area. Although C loss can occur after afforestation (Berthrong et al. 2009; Hoogmoed et al. 2012), organic C content usually increases when afforestation occurs on cropland (Guo and Gifford 2002; Paul et al. 2002; Laganière et al. 2010; Li et al. 2012). Although forest floors accumulate C quickly and mostly in labile form, the rate of mineral soil C accumulation is slow. The turnover of SOM depends on the chemical composition of the C compounds

(labile or stable), as well as environmental factors and soil properties (Jandl et al. 2007). Although more stable heavy humic fractions increase 20 years after afforestation (Del Galdo et al. 2003), the persistence of SOM mainly depends on complex interactions with its biotic and abiotic environment (Schmidt et al. 2011). Consistent with the findings, SOM content of the examined afforested sites increased compared to the data before afforestation (SOM = 1.22%; Füleky and Kovács 1993). The values are a little higher than the managed control forests (OC, LC) and form a transition among the cultivated arable land and the relict forest (RF). As suggested by the plasticity (κ_A) values, water retention is not as effective as in the relict forest, but surpasses that of cultivated land. With larger amounts of accumulated organic matter and higher plasticity, forest soils tend to support more abundant and diverse Collembola communities (Ponge et al. 2003; Bardgett et al. 2005; Potapov et al. 2017), as has been observed in the studied forest control habitats including the old-growth relict forest (RF) and also the managed stands (OC, LC). Afforestation following abandonment of farming tends to increase the spatial heterogeneity of soil resources, usually resulting in higher species richness and abundance (Arbea and Jordana 1985; Bardgett et al. 2005). Soil mesofauna, including Collembola, can show rapid increase in abundance and biomass during the first few years after afforestation (Dunger 1968; Hasegawa 2006). Community composition changes are, however, usually slower, which might be related to the distance of source habitats and the presence of connection corridors, the limited dispersal ability and, hence, the lack of colonization of certain Collembola species (Salmon and Ponge 1998; Ponge et al. 2006; Auclerc et al. 2009). Epedaphic species are more capable of migrating actively on the soil surface (Alvarez et al. 2000), while active migration of euedaphic springtails is often limited to short distances and always dependent on the population density in the soil (Sjögren 1997; Ojala and Huhta 2001). The effects of landscape heterogeneity and the characteristics of the surrounding habitats are also of decisive importance (Sousa et al. 2004; Vanbergen et al. 2007).

In the two studied plantations (LP, OP), only a few forest species were recorded, while some species characteristic to open habitats are still present. Among the species observed in the plantations, *Neanura muscorum*, *Ceratophysella luteospina*, *Entomobrya muscorum*, *Folsomia quadrioculata*, *Isotomiella minor*, and *Megalothorax minimus* can be considered as forest specialist or forest-preferring species (Auclerc et al. 2009; Vanhée and Devigne 2018). Interestingly, the last species, *Megalothorax minimus*, is present in both plantations, despite the species' poor dispersal ability as described by Ponge et al. (2006). Our results corroborate the findings of previous studies (Dunger et al. 2002; Auclerc et al. 2009), reporting rapid colonization of this neelid species. The relatively high number of open-habitat species

(e.g., *Protaphorura campata*, *Entomobrya multifasciata*, *Lepidocyrtus cyaneus*, *Pseudosinella alba*) recorded in the plantations clearly shows the impact of the surrounding habitats (cultivated fields, secondary grassland on abandoned farmland). The relatively young age of the plantations is also reflected in the dominance structure of the Collembola communities. In younger stages, the number of the non-abundant rare and accessorial species is usually lower, while distinct eudominance of singular species is often observable (Trojan et al. 1994; Vanhée and Devigne 2018) and well emphasized by the higher values of the community dominance index (CDI) in the plantations compared with the control old-growth relict forest.

Selecting suitable tree species (native vs. non-native) for afforestation is of great importance and also has a significant, long-term impact on the soil fauna (Deharveng 1996). Vegetation strongly influences Collembola diversity and abundance, mainly through the amount and quality of produced litter (Bezkorovaynaya 2005; Ma et al. 2020). Black locust is considered among the most invasive tree species in Europe (Campagnaro et al. 2018), especially in Hungary, where it comprises 25% of forest stands (Bartha 2000). Black locust has a diverse impact on soil properties, inter alia, by increasing nitrogen, nitrate, and SOM content (Lazzaro et al. 2018). The higher organic matter content is manifested in the slightly higher Collembola abundance observed in the black locust plantations when compared to the oak plantations. In terms of species richness, diversity, and equitability, their values were higher in the indigenous sessile oak plantation, which might be due to the allelopathic effect of the black locust. The secondary metabolites (e.g., phasin, robin or toxalbumins) released from the leaf litter of black locust have been proved to inhibit protein synthesis, providing unfavorable conditions for less-tolerant species (Rahmonov 2009; Lazzaro et al. 2018). Presumably, this phenomenon is responsible for the lower species richness and diversity found in the plantation of the non-native black locust as expressed by the diversity profiles (Fig. 2). In addition, community structure also shows a less even distribution among species in the black locust stand compared with the indigenous oak plantation, as emphasized in the higher CDI index.

Generally, soil acidification occurs following afforestation. The main causing factors are the increased production and input of organic acids and redistribution and sequestration of cations such as K, Ca, and Mg from soil to biomass. Relocated cations are replaced on soil exchange sites by H⁺; thus, the base saturation is lowered and the proportions of ions adsorbed to the soil exchange complex are changed (Chen et al. 2000; Jobbágy and Jackson 2003; Ritter et al. 2003; Farley et al. 2008; Shaifullah et al. 2008; Berthrong et al. 2009). In the oak plantation (OC), moderately acidic soil was found, while in the black locust

plantation (BL) slightly acidic to neutral conditions were observed. Some Collembola species have narrower, while others wider tolerance to soil pH change, and it is known that soil pH can cause great changes in Collembola community composition (Van Straalen and Verhoef 1997; Van Straalen 1998). However, the difference in pH between the two plantations is not yet noticeable in terms of species composition, as the communities of the two plantations show significant overlap in the PCoA analysis (Fig. 3). When the plantations are examined together with the controls, not only habitats but also some species are well separated along the pH gradient in the CCA biplot (Fig. 4), from the alkalophil *Brachystomella parvula* through the weakly subneutral species *Orchesella cincta* and *Lepidocyrtus cyaneus* to the acidophil *Tomocerus vulgaris*.

Conclusion

The present study demonstrated that conversion of formerly highly fertilized cultivated land to forest plantations has considerable impacts on the soil and its biota. After afforestation, Collembola communities showed clear responses in terms of composition, species richness, abundance, and diversity. Based on the community characteristics, the studied sessile oak and black locust plantations can be ranked as transitions among the cultivated arable field and the managed and old-growth forests selected as controls. Among the studied set of interacting parameters, Collembola communities were mainly driven by soil plasticity, soil organic matter, pH and phosphorus content and, to a lesser extent, by nitrogen and potassium content.

Opinions are divided on the impact forest plantations have on biodiversity (Bremer and Farley 2010; Liu et al. 2010). Depending on the tree species used, several studies found low levels of soil fauna diversity in plantations (e.g., Arbea and Jordana 1985; Deharveng 1996), while others suggest that forest plantations can contribute to restoration of forest species and thus to biodiversity conservation, especially in areas with poor agricultural soils (Hooper et al. 2005; Cunningham et al. 2015). When compared to nearby cultivated soils, our results showed improvement in terms of Collembola diversity especially in the native sessile oak plantation, suggesting the transformation of cultivated land to forest plantations of native tree species as a positive solution.

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