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Collembolan Assemblages Response to Wild Boars (*Sus scrofa* L.) Rooting in Pine Forest Soil

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Received: 16 September 2020; Accepted: 19 October 2020; Published: 22 October 2020

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Abstract: Collembola are an important component of soil communities in all terrestrial ecosystems. In temperate coniferous forests, they are one of the most numerous invertebrate groups, and disturbances that change their density and structure may have negative effects on soil fertility and productivity. Our goal was to determine whether intensive rooting in the forest floor by wild boars affects edaphic Collembola. Soil samples from three paired rooted and non-rooted plots in Scots pine stands were taken twice a year to study the impact of such bioturbation on forest collembolan assemblages. Substantial changes in the taxonomic and functional structure of the collembolan assemblages were identified in all disturbed plots. The abundance and number of species significantly decreased in the bioturbated forest floor. The shares of atmobiotic and hemiedaphic springtails increased at the expense of epedaphic forms. Most of the differences were evident shortly after grubbing but were not significant a few months later. The decline in moisture in disturbed soil could be an explanatory factor causing the differences in the structure and abundance of collembolan assemblages between the bioturbated and intact plots. Our study revealed that large mammals ubiquitous in forest ecosystems can be an important disturbing factor for soil microarthropods. Intensive wild boar rooting in the forest floor had a strong negative effect on the occurrence and abundance of Collembola. This kind of bioturbation also modified the functional structure of assemblages, which in turn may have important consequences for the soil food web and above- and belowground interactions.

Keywords: bioturbation; mesofauna; soil moisture; Scots pine; temperate forest

1. Introduction

Collembola play an important role in forest ecosystems because they affect processes such as decomposition, nutrient cycling, and soil carbon storage and thereby influence soil fertility and productivity [1–4]. The composition and structure of collembolan assemblages are in turn strongly affected by the soil environment, namely, soil moisture and temperature [5–7], pH [8–10], and soil porosity and bulk density [11]. They are also deeply influenced by changes in soil organic matter availability and humus form [12,13]. Therefore, any disruption causing a change in one of these factors may result in the modification of the taxonomic and functional structure of collembolan assemblages. Research on the disturbances caused by forest management practices such as tree harvesting, harvest residue removal, site preparation, or prescribed burning has revealed highly variable but mainly negative responses of edaphic Collembola [14–17]; but see [18]. This result is also true for large-scale abiotic natural disturbances, such as windthrow and fire [19,20].

Large mammals numerous in forest ecosystems may also affect the soil biota by trampling, dunging, or grubbing, but detailed research on their activities is rare [21,22]. Wild boar (*Sus scrofa* L.) are one of the most widely distributed wild mammals currently present on almost all continents [22].

Wild boar, in search of food consisting of seeds and plant roots, small vertebrates, and invertebrates [23], intensely grub the forest floor, causing considerable disruption to the soil environment. They breaks through the vegetation and typically affect 15–50 cm of the upper soil horizon. The study of the effects of wild boar rooting on soil properties revealed changes in soil moisture, some nutrient contents, and mineralisation rates [22], but see [24]. Higher microbial biomass carbon in rooted than non-rooted plots in mixed hardwood forest was reported by Risch et al. [25], while Mohr et al. [21] reported lower biomass in oak forest. Wild boar may also have a harmful effect on soil invertebrates, as evidenced by studies in tropical rainforests [26,27]. Therefore, attempts have been made to develop programmes and procedures for monitoring the impact of increasing wild boar populations on biodiversity [28].

In Scots pine forests, prevailing in vast areas of lowland Poland, soil invertebrate communities are dominated by mesofauna, i.e., Acarina and Collembola. Nevertheless, no detailed studies have been conducted to date focusing on the effect of bioturbation by wild boar on microarthropod communities of temperate forests. The objective of this study was to assess the response of collembolan assemblages to wild boar activity in Scots pine stands on podzols [29]. Specifically, we ask whether intensive rooting changes the composition, structure, and abundance of edaphic collembolan assemblages. We have applied a species-level examination and assessed the functional structure of assemblages because this approach offers ecologically relevant information on the assemblage's response to disturbances [30,31]. In the case of Collembola, life forms (*sensu* Gisin [32]) are clearly related to the trophic position of species and their functional role in ecosystems [33], which predisposes the group to being a good tool for bioindication.

2. Materials and Methods

2.1. Study Sites and Sampling

The study was conducted in Scots pine monoculture in Kolumna Forest District located on a vast periglacial plain with inland dunes at elevations ranging from 130 to 280 m a.s.l. in central Poland. The mean air temperature is 7.5–8 °C, the annual rainfall is 550–600 mm, and the vegetation growth period lasts from 210 to 220 days [34].

We chose three stands situated in Forest Range Mogilno (51°37′ N, 19°18′ E) at a distance of 1–2 km from each other. The forest stands were classified as typical Leucobryo-Pinetum growing on podzols with litter layer depths ranging between 8 and 12 cm. These stands represent the outbreak centre of the great web-spinning pine sawfly *Acantholyda posticalis* Mats, for which pre-imaginal stages in great numbers occur in the litter and soil. The forest floor under the tree canopies is intensively grubbed by wild boars in search of the larvae of this insect, especially in winter and early spring, when food in agricultural areas is scarce. In late spring, we established a paired-plot experimental design with uniformly rooted (bioturbation plot—B) and non-rooted sites (control plot—C) in each of the three stands. All plots were 5 × 5 m in size. In microarthropod studies, in homogeneous environments such as pine forests in poor habitats, small research areas provide reliable data for community assessment [35]. In the disturbed plots, the rooting depth varied but was generally deeper than 10 cm, the protective ground vegetation was destroyed and moved aside, and the surface microtopography was changed as a result. The non-rooted plots were selected to be in close proximity (approximately 10 m) to the plots where rooting occurred. In this type of forest, the traces of bioturbation can be seen even after three years (personal observation, according to the opinion of foresters), so it can be assumed that our control plots have been left intact by the boars for over three years.

Soil sampling for fauna extraction was conducted just after plot establishment in early June and repeated in late September 2018. From each plot, six sets of samples consisting of five soil cores were collected with a metal cylinder (diameter of 5 cm) to a depth of 15 cm. The cores were taken in the central part of the plots, and the top litter layer and vegetation cut by the cylinder were also included in samples and put immediately into plastic bags. In the laboratory, the soil fauna were extracted in a Tullgren apparatus with 25 W light bulbs for two weeks and stored in 70% ethanol. Collembola specimens taken from ethanol were elaborated sorted depending on body size; the larger specimens were examined under a binocular microscope (Olympus SZX9, Olympus Optical CO, LTD, Japan) under a magnification of 50× (Warsaw, Poland), while the smallest specimens were put into KOH 50% and chlorophenol for clarification, then onto slides and were identified under a light microscope (Zeiss Axiolab, Carl Zeiss, Germany) under a magnification of 400× (Warsaw, Poland). Collembola were identified to species or higher taxa (in the case of juvenile specimens) using taxonomic keys [36–42] and counted.

The classification of Babenko et al. [43] and Rusek [44] was applied to distinguish the following life forms: atmobiotic (a), epedaphic (ep), hemiedaphic (h), and euedaphic (eu).

Based on life form and taxonomic identity, four functional leagues of Collembola with presumed ecosystem functions were outlined by Potapov et al. [33]. The first functional league controls microbial communities affecting the dynamics of the earliest stages of litter decomposition. The second league regulates the densities of microorganisms and microbivores and possibly also affects the rate of wood decomposition. The third, controlling microbial communities, influences the structure and mineralisation rate of litter. The fourth league influences nutrient uptake by roots, the microbial community in the rhizosphere, and the decomposition of soil organic matter. Knowledge of changes in the functional structure of collembolan assemblages provides insight into soil processes.

Six soil samples for the measurement of water content were taken with a metal cylinder (diameter = 5 cm, length = 15 cm) from all study plots in early June. In the laboratory, the soil cores were weighed with an accuracy of 0.001 g, dried at 105 °C for 48 h until the samples attained a constant mass, and then reweighed.

2.2. Data Analysis

The completeness of the collembolan assemblage list was evaluated with an estimator of sample coverage [45]. The soil moisture in the rooted and control plots was compared using one-way analysis of variance ANOVA. To assess the effect of intensive rooting on collembolan assemblages, we compared their abundance, species diversity, species composition, and life form structure on rooted and non-rooted plots. A power analysis [46] showed that the number of samples was sufficient to compare bioturbated and control plots, according to soil moisture, collembolan abundance, and the number of species (Table S1 in Supplementary Materials). The abundance and number of species were compared using two-way ANOVA, with plot type (control, bioturbated) and season (spring, autumn) as factors. Since the number of species recorded is strongly dependent on the number of individuals tested, we used a comparison of the species accumulation curve using rarefaction of Hill numbers (of 0, 1, and 2 orders) based on abundance data [45]. This method allowed us to evaluate the biological diversity with little influence of different sizes of species pools in each experimental variant. For soil moisture and abundance, the data were logarithmically transformed (log 10) to attain normality and homogeneity of variance. We used nonmetric multidimensional scaling (NMDS) to examine differences in the composition of the collembolan assemblages with 1000 permutations. NMDS was based on a dissimilarity matrix constructed with the Bray-Curtis index. We excluded rare species, i.e., represented by fewer than five individuals and observed in fewer than three plots from the ordination, but we included juvenile forms of Collembola since they composed a substantial part of the assemblages. The number of individuals in each plot was square root transformed to reduce the influence of the most numerous species. To confirm the statistical significance of the observed differences, one-way permutational multivariate analysis of variance with 1000 permutations (PERMANOVA) was performed, even though the variance of the dissimilarity index in the control plots (spring) was significantly lower than that in the other plots. PERMANOVA is generally robust to moderate heterogeneity of variance in balanced study designs [47,48]. To determine which assemblages significantly differed, a pairwise test was performed. We analysed a contingency table containing the number of individuals belonging to a given life form in each plot type using a chi-squared test of independence. The differences in life form structure were visualised with a mosaic plot. The analysis was performed using R version 3.6.1 (R Developmental Core Team, Vienna, Austria) (functons: aov, chisq.test) [49] with the following packages: iNEXT v. 2.0.20 (functions: iNEXT, ggiNEXT) [50], vegan v. 2.5-5 (functions: vegdist, metaMDS, adonis) [51], car v. 3.0-3 (functions: shapiro.test, leveneTest) [52], and vcd v.1.4-4 (function: mosaic) [53].

3. Results

We recorded a total of 2922 individuals belonging to 38 taxa (Table 1). The highest number of taxa per plot was 24, and the lowest was 20. The sample coverage exceeded 0.97, suggesting that a substantial proportion of the species present in the area was sampled.

Table 1. Species list, life forms, and mean abundance (ind. m^{-2}) of Collembola in plots bioturbated by wild boars (B1, B2, B3) and control plots (C1, C2, C3). Life forms: a, atmobiotic; ep, epedaphic; eu, euedaphic; h, hemiedaphic. The life form classification of taxa is according to Babenko et al. [43], Rusek [44], and Potapov et al. [33].

Taxa	Life Form	C1	C2	C3	B1	B2	B3
Xenylla maritima Tullberg, 1869	ep	450	400	50	267	233	300
Xenylla sp. juv.	ep	67	-	-	-	-	-
Willemia anopthalma Börner, 1901	eu	33	17	33	-	-	-
Friesea claviseta Axelson, 1900	ep	533	50	1717	-	133	-
F. truncata Cassagnau, 1958	ep	950	50	-	317	-	67
Friesea sp. juv.	ep	17	17	-	17	17	-
Pseudachorutes dubius Krausbauer, 1898	ep	-	33	17	-	-	17
Pseudachorutes corticicolus (Schäffer, 1896)	ep	17	-	-	-	-	-
Pseudachorutes sp. juv.	ep	33	17	17	33	-	17
Micranurida pygmea Börner, 1901	h	50	-	17	-	17	-
Neanura muscorum (Templeton, 1835)	h	133	283	117	567	233	433
Neanuridae juv.	h	200	483	133	17	133	50
Micraphorura absoloni (Börner, 1901)	eu	-	33	17	-	50	33
Mesaphorura yosii Rusek, 1967	eu	-	-	33	-	-	-
Anurophorus atlanticus Fjellberg, 1974	ep	-	17	500	17	-	17
A. laricis Nicolet, 1842	ep	-	33	-	17	100	17
A. septentrionalis (Pallisa, 1966)	ep	3483	-	683	83	-	1083
Anurophorus sp. juv.	ep	300	17	417	33	-	550
Folsomia quadrioculata (Tullberg, 1871)	h	17	-	800	-	-	33
Proisotoma minima (Tullberg, 1871)	h	-	-	-	-	17	-
Isotomiella minor (Schäffer, 1896)	eu	67	100	600	33	33	100
Parisotoma notabilis (Schäffer, 1896)	h	1767	1467	4383	850	350	783
Desoria tolya Fjellberg, 2007	ep	633	17	467	583	233	233
Desoria trispinata (Mac Gillivray, 1896)	ep	-	-	3850	350	-	183
Desoria sp. juv.	ep	2817	3367	3233	17	717	267
Tomoceridae juv.	ep	-	-	-	-	17	-
Orchesella bifasciata Nicolet, 1841	a	-	83	133	50	17	183
O. flavescens (Bourlet, 1839)	a	-	17	-	-	-	-
O. multifasciata (Stscherbakow, 1898)	a	-	-	-	83	-	-
Orchesella sp. juv.	a	-	17	33	-	-	-
Entomobrya corticalis (Nicolet, 1841)	a	-	-	-	33	33	267
E. multifasciata (Tullberg, 1871)	a	67	-	-	67	-	-
Willowsia buski (Lubbock, 1869)	a	-	-	-	-	17	-
Lepidocyrtus lignorum (Fabricius, 1775)	ep	83	467	1467	83	100	-
Pseudosinella zygophora (Schille, 1908)	h	100	267	-	-	-	-
Entomobyidae juv.	a	33	67	-	83	50	17
Megalothorax minimus (Willem, 1900)	eu	-	-	33	-	-	-
Arrhopalites sp. juv.	h	-	17	-	-	17	-

The soil moisture was lower in the grubbed plots than in the control plots (Figure 1). The average water content was 5.56% and 8.91%, respectively (two-way ANOVA: SS = 0.36, F = 27.72, $p < 0.0001$).

Differences among replicates were nonsignificant (SS = 0.064, F = 2.48, $p = 0.105$), and there was no interaction between plot type and replicate (SS = 0.01, F = 0.37, $p = 0.6$).

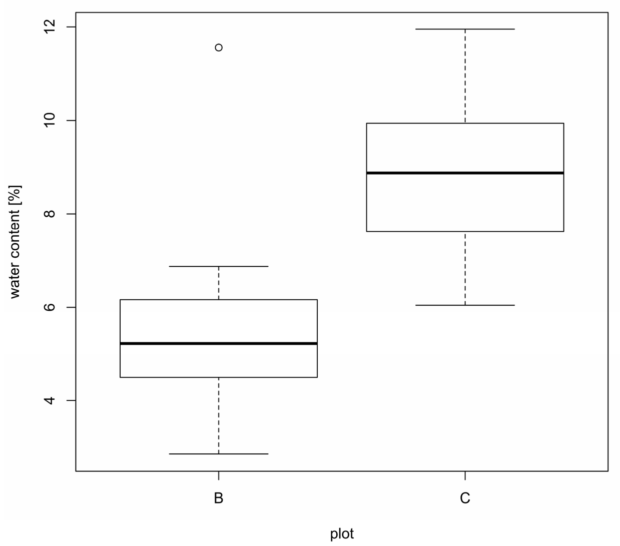

Figure 1. Soil moisture in plots bioturbated by wild boar (B) and control plots (C).

The abundance of Collembola in plots bioturbated by wild boar was significantly lower than that in control plots (two-way ANOVA: SS = 1508.0, F = 40.25, $p < 0.0001$) (Figure 2). There was no significant difference between spring and autumn (SS = 140.0, F = 3.74, $p = 0.06$), and there was no interaction between season and rooting (SS = 46.7, F = 1.25, $p = 0.27$). The average abundance in the grubbed plots was more than 3600 per m^2, while that in the non-grubbed plots was approximately 12,600 per m^2 (Figure 2).

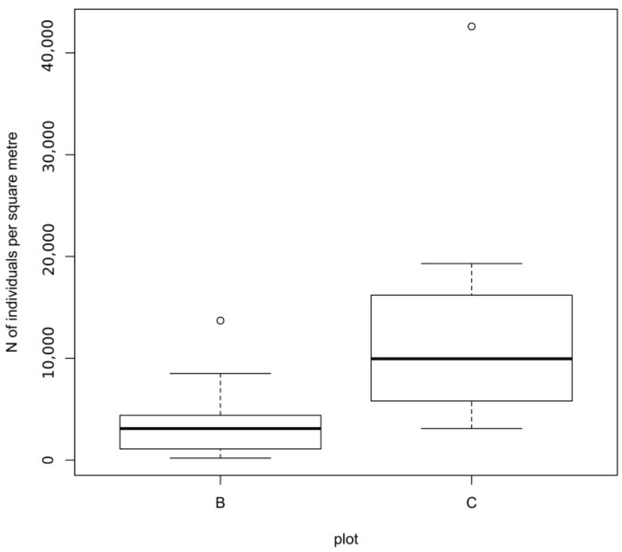

Figure 2. Abundance of Collembola in plots bioturbated by wild boar (B) and control plots (C).

Composition of the collembolan assemblages in the rooted plots differed distinctly from those in the control plots (Figure 3). However, this difference was noticeable only for spring, while the structure of the collembolan assemblages during autumn was similar in both types of plots. The differences were confirmed by PERMANOVA (F = 7.23, $p < 0.001$), and the model explained 40.4% of the variance in the data. The assemblages in the bioturbation-spring (BS) plots differed from all other assemblages (control-spring (CS): F = 8.74, $p < 0.006$; control-autumn (CA): F = 5.61, $p > 0.006$; bioturbation-autumn

(BA): F = 6.17, $p > 0.006$) as well as the CS assemblages (CA: F = 10.49, $p > 0.006$; BA: F = 11.97, $p > 0.006$). Autumn data revealed no significant differences between the BA and CA plots (F = 2.36, $p = 0.126$).

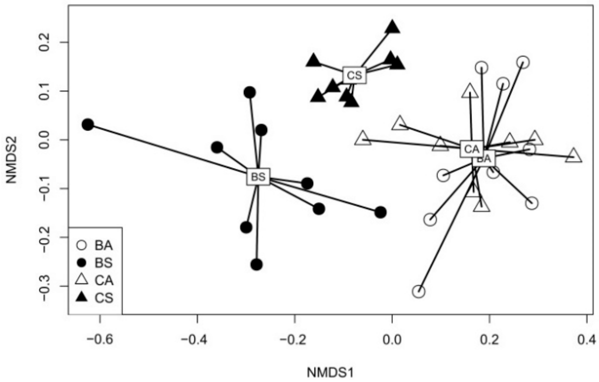

Figure 3. Nonmetric multidimensional scaling (NMDS) ordination plot of the dissimilarities in the collembolan assemblages in control and bioturbated plots.

The average number of species per sample was significantly higher in the control plots than in the rooted plots (two-way ANOVA SS = 81.0, F = 15.25, $p = 0.0005$) (Figure 4). Samples collected in autumn were richer in species than those collected in spring (SS = 87.11, F = 16.40, $p = 0.003$). However, there was no significant interaction between disturbance and season (SS = 0.44, F = 0.08, $p = 0.78$).

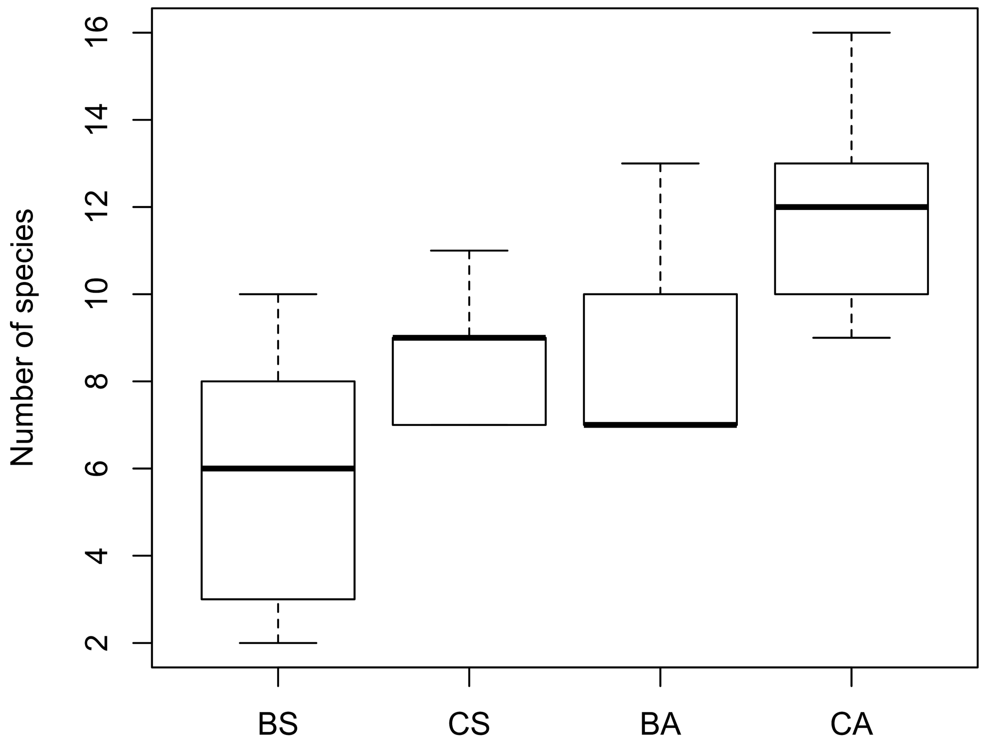

Figure 4. Average number of species per sample in the control and bioturbated plots in spring and autumn. BS, bioturbation plots—spring; CS, control plots—spring; BA, bioturbation plots—autumn; CA, control plots—autumn.

Total species richness achieved the highest values on the control plots in autumn and the lowest on bioturbated plots in spring (Figure 5). However, exponential Shannon's and inverse Simpson's indexes reached higher values on bioturbated plots than on control plots both in spring and autumn.

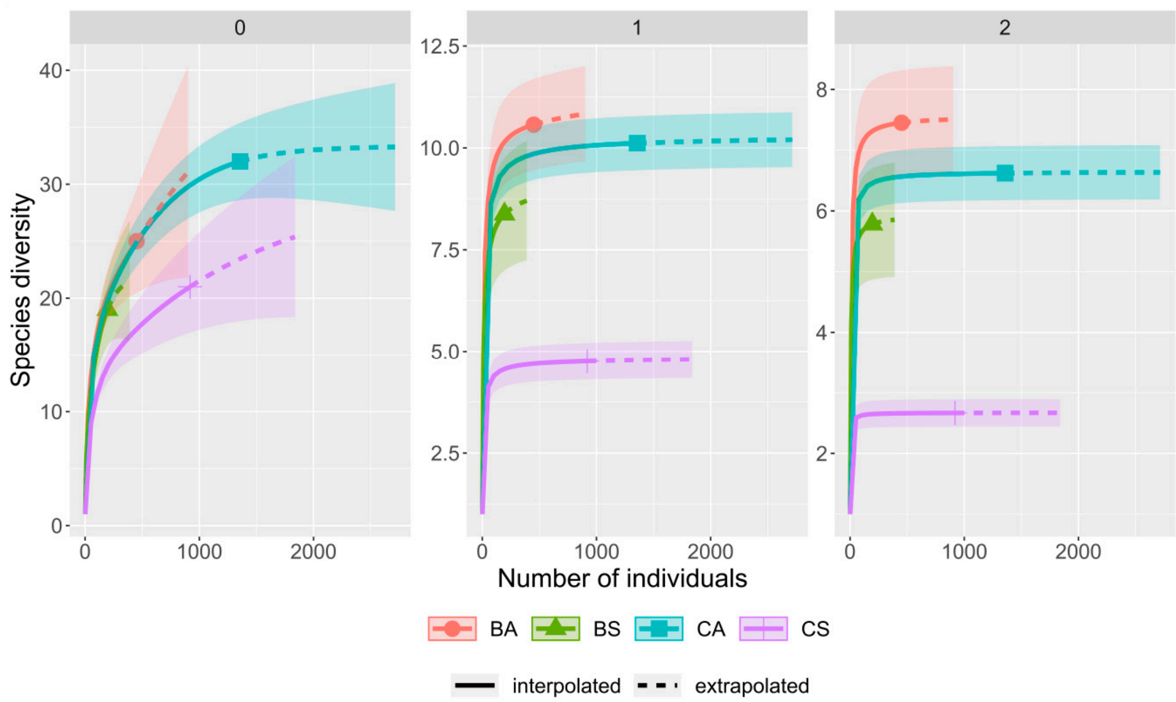

Figure 5. Accumulation curves of the Hill numbers of the collembolan assemblages in control and bioturbated plots. BS, bioturbation plots—spring; CS, control plots—spring; BA, bioturbation plots—autumn; CA, control plots—autumn. 0, ^{0}D species richness; 1, ^{1}D exponential Shannon's entropy index; 2, ^{2}D inverse Simpson's index.

Rooting by wild boars significantly influenced the life form structure of the assemblages compared to those in the control plots (chi-squared = 110.73, df = 3, $p < 0.0001$). The abundance of atmobiotic and hemiedaphic species was higher in grubbed plots, while the abundance of epedaphic Collembola was lower (Figure 6).

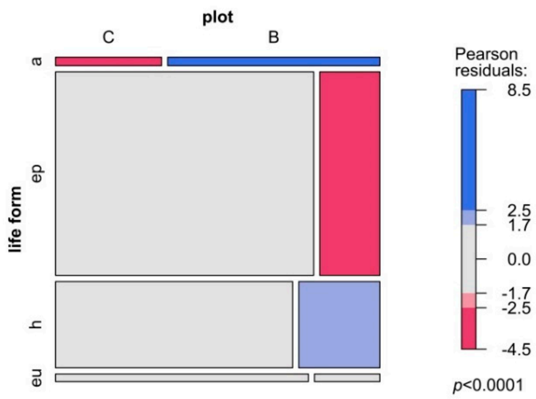

Figure 6. Mosaic plot of collembolan life form occurrence in control plots (C) and in plots bioturbated by wild boar (B). Life form code: a, atmobiotic; ep, epedaphic; h, hemiedaphic; eu, euedaphic.

4. Discussion

Our results show that rooting by wild boars had a strong negative effect on forest collembolan assemblages inhabiting the litter and soil. The taxonomic and functional structure of the assemblages was altered, and the populations of many species were decimated in all plots disturbed by grubbing activity. This finding corresponds to those of Mohr et al. [21], who reported that soil bioturbation by wild boar and red deer had a negative effect on the abundance of saprophagous soil arthropods such as Diptera larvae, Isopoda, Diplopoda, predatory Arachnida, Coleoptera, and Chilopoda in beech forests. Additionally, Taylor et al. [27] showed that wild boar activity caused a significant decline in macroinvertebrate density in lowland tropical forests. The response of soil microarthropods to disturbances caused by this mammal was studied only in Hawaiian rainforests, where soil communities are dominated by Collembola [26]. The research concerned the regeneration of soil communities after the removal of feral pigs. Based on the rate of regeneration of species richness and abundance of collembolan assemblages, it was possible to indirectly assess the values of these parameters before the disturbance. In both studied types of forests, springtails proved to be the most sensitive invertebrate group to soil damage by wild boar, as populations of many species were decimated and some taxa disappeared completely [26]. We are not aware of any other research on the impact of grubbing on soil micro-invertebrates, but some forest management practices, such as site preparation, seem to have similar effects on soil biota as wild boar activity. For example, Bird et al. [14] found significantly lower Collembola abundance in post-harvest plots where mechanical or hand bedding was performed in comparison to plots without a site preparation treatment in a loblolly pine plantation. Similarly, a negative impact of mounding and scalping (removing almost all forest floor organic material) on the density of forest collembolan communities was reported by Berch et al. [54] in conifer plantations.

The striking differences in the structure and abundance of collembolan assemblages between the rooted and non-rooted plots detected in our study may have been caused by a decrease in the moisture of the soil disturbed by wild boar rooting. The significantly lower actual soil moisture of the grubbed plots revealed by our measurements was in accordance with the results of studies on the effect of wild boar activity in hardwood forests, which documented a reduction in soil moisture at the grubbing sites [25]. Soil moisture has often been reported to be the most important factor affecting the structure and function of soil fauna [5,6,55–58]. Edaphic Collembola in pine forests on podzols seem to be adapted to temporary drought events and able to survive even extreme conditions; however, they may not be able to cope with very long drought periods [57,59,60]. In most field experiments, extreme drought treatments induced a negative change in the abundance and density of soil Collembola (e.g., [5,57,58]). The observed overall decrease in Collembola abundance in the plots rooted by wild boars in our study was expected and consistent with the abovementioned experiments. In addition to the noteworthy reduction in springtail abundance, our study also showed distinct changes in the taxonomic structure of collembolan assemblages owing to bioturbation, which was particularly evident shortly after grubbing, i.e., in spring. Moreover, the life form structure of the assemblages was also significantly altered since more atmobiotic and hemiedaphic springtails at the expense of epedaphic species were recorded in the plots rooted by wild boars. These findings correspond to the effect of drought manifesting in changes in the dominance structure of Collembola communities revealed by Lindberg et al. [57], while a decrease in epedaphic life forms in experiments with induced drought was reported by Flórián et al. [60].

The strong decline in abundance and changes in the structure of collembolan assemblages may also be due to the reduction of plant cover on bioturbated plots. The mosses predominating in the pine forest floor provide microhabitats and stable microclimate for forest soil invertebrates by mitigating the temperature and moisture amplitudes [61]. The experimental removal of the moss layer in boreal forests had a strong negative effect on Collembola abundance and diversity regardless of the age of the studied tree stands [62]. Additionally, the structure of assemblages distinctly changed since euedaphic and epedaphic forms significantly decreased in number in the removal treatment. These conclusions are consistent with our results, but the difference is that in our grubbed plots, only the reduction of the epedaphic form was significant. However, in both cases, the high sensitivity of Collembola to biotic disturbance of the forest floor was well documented. Disturbance to litter has also been identified as the main cause of the strong decline in Collembola density in Hawaiian rainforests damaged by grubbing and trampling by invasive pigs [26]. When assessing the influence of wild boars on forest ecosystems, it is worth noting that these animals very often returned to previously bioturbated sites to re-disturb, so reduced litter cover may not have a chance to regenerate. As a consequence, adverse changes in the soil environment, especially in nutrient-poor habitats, may occur in disturbed areas [63].

5. Conclusions

The activity of large mammals in forest ecosystems can substantially affect belowground microarthropod communities. We showed that intensive wild boar rooting caused substantial changes in the taxonomic and functional structure of collembolan assemblages. The abundance and number of species was significantly decreased in all bioturbated plots. Moreover, the share of atmobiotic and hemiedaphic springtails increased at the expense of edaphic forms. Differences were evident shortly after grubbing but were not significant a few months later. The decline in moisture in soil disturbed by wild boars could be an explanatory factor causing the differences in the structure and abundance of collembolan assemblages between the rooted and non-rooted plots. Therefore, bioturbation caused by wild boar may have important consequences for the soil food web and processes essential for soil fertility and the productivity of temperate coniferous forests.

Supplementary Materials: The following are available online at http://www.mdpi.com/1999-4907/11/11/1123/s1, Figure S1: Plots bioturbated by wild boar (photo M. Sławski), Figure S2: Control plot (photo M. Sławski), Table S1: Results of power analysis.

Author Contributions: Conceptualisation and methodology, M.S. (Marek Sławski) and M.S. (Małgorzata Sławska); fieldwork, M.S. (Marek Sławski) and M.S. (Małgorzata Sławska); Collembola identification, M.S. (Małgorzata Sławska); data analysis, M.S. (Marek Sławski); writing—original draft preparation M.S. (Marek Sławski) and M.S. (Małgorzata Sławska). All authors have read and agreed to the published version of the manuscript.

Funding: This study research was funded by the Polish State Forests (grant number OR.217.3.19.2017).

Conflicts of Interest: The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, or in the decision to publish the results.

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