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

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Research

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Abstract

Background:

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.

Results:

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.

Conclusions:

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 caused also the modification to the functional structure of assemblages, which in turn may have important consequences for soil food web and above- and below-ground interactions.

Background

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 (Seastedt and Crossley, 1980; Rusek, 1998; Eisenhauer et al., 2011; Filser et al., 2016). The composition and structure of collembolan assemblages are in turn strongly affected by the soil environment, namely, soil moisture and temperature (Petersen, 2011; Xu et al., 2012; Russell and Gergóc, 2019), pH (Hägvar, 1984; Loranger et al., 2001; Salamon and Alphei, 2009), and soil porosity and bulk density (Lindo and Visser 2004). They are also deeply influenced by changes in soil organic matter availability and humus form (Cassagne et al., 2003; Ponge, 2013). 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 have revealed
highly variable but mainly negative responses of edaphic Collembola (Bird et al., 2004; Malmström et al., 2009; Rousseau et al., 2018, Rousseau et al., 2019) but see (Setälä et al. 2000). This result is also true for large-scale abiotic natural disturbances, such as windthrow and fire (Čuchta et al., 2013, Čuchta et al., 2019).

Large mammals numerous in forest ecosystems may also affect the soil biota by trampling, dunging or grubbing, but detail research on their activities are rare. Wild boar (*Sus scrofa* L.) is one of the most widely distributed wild mammals currently present on almost all continents (Barrios-Garcia and Ballari 2012). Wild boar, in search of food consisting of seeds and plant roots, small vertebrates and invertebrates, grub intensely the forest floor causing considerable disruption to the soil environment. It breaks through the vegetation and typically affects 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 (Barrios-Garcia and Ballari 2012), but see (Groot Bruinderink and Hazebroek 1996). Higher microbial biomass carbon in rooted than non-rooted plots in mixed-hardwood forest was reported by Risch et al., (2010), while Mohr et al., (2005) reported lower biomass in oak forest.

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 studies have been conducted so far focussing on the effect of bioturbation by wild boar on microarthropod communities. The objective of this study was to assess the response of collembolan assemblages to wild boar activity in Scots pine stands on Podzols (IUSS Working Group WRB 2015). Specifically, we ask whether intensive rooting changes the composition, structure and abundance of edaphic collembolan assemblages.

**Methods**

**Study sites and sampling**

The study was conducted in Scots pine monoculture in Kolumna Forest District (51°37´ N, 19°18´ E) 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 ºC, the annual rainfall 550–600 mm, and the vegetation growth period lasts from 210 to 220 days (Lorenc, 2005).

We chose three stands 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 areas (control plot - C) in each of the three stands. All plots were 5 × 5 m in size. 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 to the plots where rooting occurred. In this
type of forest, the traces of bioturbation can be seen even after three years, so it can be assumed that our control plots have been 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 method used for Collembola extraction and species and life-form identification was described by Sławski and Sławska (2019). Six soil samples of the same size for the measurement of water content were taken 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 hours until the samples attained a constant mass and then reweighed.

Data analysis

The completeness of the collembolan assemblage list was evaluated with an estimator of sample coverage (Chao and Jost 2012). The soil moisture in the rooted and control plots was compared using one-way 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. The abundance and number of species were compared using two-way ANOVA, with plot type (control, bioturbated) and season (spring, autumn) as factors. For soil moisture and abundance, the data were logarithmically transformed (log10) to attain normality and homogeneity of variance. We used nonmetric multidimensional scaling (NMDS) to examine differences in the composition of the collembolan assemblages. 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 down-weight influence of the most numerous species. To confirm statistical significance of the observed differences one-way permutational multivariate analysis of variance (PERMANOVA) was performed, despite 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 (Anderson 2001; Anderson and Walsh 2013). 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 with use of a chi-square test of independence. The differences in life form structure were visualised with a mosaic plot. The analysis was performed using R 3.6.1 (R Core Team. 2020) with the following packages: iNEXT (Hsieh et al. 2016), vegan (Oksanen et al. 2019), car (Fox and Weisberg 2019), and vcd (Meyer et al. 2006).

Results
We recorded a total of 2,922 individuals belonging to 38 taxa (Table). 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. 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. Life-form classification is according to Babenko et al. (1988) and Potapov et al. (2016).
| 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  | -   | -   |
| Taxa                              | Life form | C1 | C2  | C3  | B1 | B2 | B3 |
|----------------------------------|-----------|----|-----|-----|----|----|----|
| 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 | -   | -   | -  | -  | -  |

The soil moisture was higher in the grubbed plots than in the control plots (Fig. 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).

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) (Fig. 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 3.6 thousand per m², while that in the non-grubbed plots was approximately 12.6 thousand per m² (Fig. 2).

Composition of the collembolan assemblages in the rooted plots differed distinctly from those in the control plots (Fig. 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).
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) (Fig. 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). Total species richness achieved the highest values on the control plots in autumn and the lowest on bioturbated plots in spring (Fig. 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. Accumulation curves suggest that lower species richness is a result of the low number of individuals in the grubbed plots and possible lower species detection.

Rooting by wild boars significantly influenced the life-form structure of the assemblages compared to those in the control plots (Chi square = 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 (Fig. 6).

**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. (2005), 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. We are not aware of any other research on the impact of grubbing on soil 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. (2004) 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., (2007) 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 (Risch et al. 2010). Soil moisture has often been reported to be the most important factor affecting the structure and function of soil fauna (Verhoef and van Selm, 1983; Pflug and Wolters, 2001; Lindberg et al., 2002; Tsiafouli et al., 2005; Petersen, 2011; Xu et al., 2012). 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 (Lindberg et al., 2002; Lindberg and Bengtsson, 2006; Flórián et al., 2019). In most field experiments, extreme drought treatments induced a negative change in the abundance and density of soil Collembola (e.g. Lindberg et al., 2002; Tsiafouli et al., 2005; Petersen, 2011). 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., (2002), while a decrease in epedaphic life forms in experiments with induced drought was reported by (Flórián et al. 2019).

Revealed by our study 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 microhabitat and stable microclimate for forest soil invertebrates by mitigating the temperature and moisture amplitudes (Blok et al. 2011). 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 studied tree stands (Bokhorst et al. 2014). Also, the structure of assemblages distinctly changed since euedaphic and epedaphic forms significantly decreased in numbers in removal treatment. These conclusions are consistent with our result but the difference is that in our grubbed plots only reduction of epedaphic form was significant. However, in both cases, the high sensitivity of Collembola to biotic disturbance of the forest floor was well documented.

Conclusions

The activity of large mammals in forest ecosystems can substantially affect below-ground 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 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 soil food web and processes essential for soil fertility and the productivity of temperate coniferous forests.

Abbreviations

BS
Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable

Availability of data and material

The datasets used and/or analysed during the current study are available from the corresponding author on reasonable request.

Competing interests

The authors declare that they have no competing interests.

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Authors' contributions

M.Si. conducted data analysis; M.Sa. conducted Collembola identification. All authors participated in study design, fieldwork, interpreting the results and preparing the manuscript. All authors read and approved the final manuscript.

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Not applicable.

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Figure 1

Soil moisture in plots bioturbated by wild boar (B) and control plots (C)
Figure 2

Abundance of Collembola in plots bioturbated by wild boar (B) and control plots (C)
Figure 3

Nonmetric multidimensional scaling (NMDS) ordination plot of the dissimilarities in the collembolan assemblages in control and bioturbated plots.
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.
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, 0D species richness; 1, 1D exponential Shannon's entropy index; 2, 2D inverse Simpson's index. However, exponential Shannon's and inverse Simpson's indexes reached higher values on bioturbated plots than on control plots both in spring and autumn. Accumulation curves suggest that lower species richness is a result of the low number of individuals in the grubbed plots and possible lower species detection.
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

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