



Edaphic Collembola assemblages of European temperate primeval forests gradually change along a forest-type gradient



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ABSTRACT

The Białowieża Primeval Forest is the largest remnant of temperate virgin forest in central Europe. To investigate the relationship between forest type and edaphic Collembola assemblages, we established 36 study sites in the Strict Nature Reserve that represented the most valuable old growth forest stands and included most of the variability in forest type. The faunas of the humid and boggy deciduous forests were more abundant than those of the moderately humid forests. Three primary groups of assemblages were revealed by multivariate analysis to be typical of the following forest types: (i) coniferous bog forest, (ii) humid and moderately humid coniferous forest, and (iii) deciduous forest. Collembola assemblages were only moderately related to specific forest types but instead changed continuously along the environmental gradient that they formed. At the species level, the correlations to forest type were stronger, and approximately one-third of the collembolan species qualified as significant forest type indicators; both forest specialists and forest generalists were identified. Six species were revealed to be forest generalists because they indicated a wide spectrum of forest types. Nine species were significantly correlated with four to six forest types and were identified as broad specialists, and seventeen indicator species were associated with one, two or three forest types and were classified as narrow specialists. Because the correlation between the edaphic Collembola faunas and forest type revealed a gradual rather than categorical change in the community assemblages, we suggest that this relationship be considered in the development of future forest monitoring programmes.

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1. Introduction

Forests are the largest terrestrial land cover type in Europe and occupy more than 40% of the area of the European Union [1]. However, management of varying intensity has altered almost all forest stands [2], and unmodified primeval remnants currently represent less than 1% of the forested area of Europe [3]. Such sites provide excellent research opportunities to study natural processes due to the lack of any human intervention. Moreover, these sites have an important role as reference baselines for nature-based silviculture and can be used, for example, to develop biodiversity guidelines for managed forests [3,4].

Collembola (springtails) are among the most abundant

arthropod groups in temperate forest soils [5], and because they are ubiquitous in soils and highly sensitive to many environmental parameters [6], they are widely used as bioindicators of forest systems [7–15]. Research on the Collembola of primeval forests can enhance the understanding of edaphic microarthropod communities in their natural state and can serve as reference points and baselines to assess and direct the cultivation of managed forests. However, despite the benefits of research in primeval stands, studies on silvicolous communities of Collembola are conducted primarily in secondary forests or forest plantations. Therefore, information on the structure of pristine springtail faunas is limited, and little is known of the influence of soil characteristics and stand traits on these communities. However, the use of pristine models as a reference for the condition of managed forests is applicable only for stands of the same forest type. For the Collembola in pristine stands to be used as a reference, it must first be determined whether springtail communities are appropriate indicators of forest types, i.e., whether a characteristic assemblage of species in

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pristine stands is associated with a particular forest type. The evidence of a close relationship between edaphic Collembola and forest vegetation is substantial [e.g., [16–25]], but the relationship between these animals and forest type remains a matter of debate [26].

The Białowieża Primeval Forest is situated at the border between the republics of Poland and Belarus and is the largest remnant of the immense virgin forest that once stretched across the European Plain. The stands are rich in tree species, and their age structures are spatially diverse. Furthermore, the continuity of plant cover and more than 90 years of strict protection have resulted in an almost pristine forest community; i.e., the resident plant and animal communities are assumed to have resulted from natural ecosystem processes only [27]. In the strictly protected core area of Białowieża Forest (the Strict Nature Reserve), in which no management measures are allowed, the rich geological and soil diversity is reflected in the wide variety of vegetation. Thus, twelve Polish lowland forest types are represented in the Strict Nature Reserve [28], and they provide an ideal research opportunity for studying the effects of forest type within a relatively small region.

In this study, we assume that the development of undisturbed forests in the Strict Nature Reserve of the Białowieża Forest led to the development of Collembola communities that are well adapted to and typical of the resident forest types. Because the investigated forest stands were all within the same region, we ignored potential biogeographic differences among the communities (see Refs. [18,29] for geographical differentiation among the collembolan faunas). Our basic hypothesis was that forest type significantly determines the abundance of individual Collembola species and the abundance, diversity and structure of Collembola communities. Specifically, we asked the following questions:

1. Does the structure of Collembola assemblages (i.e., total abundance, diversity, and dominance structure) differ significantly among the twelve forest types in the Białowieża Strict Nature Reserve?
2. When differences are detected, which species contribute most to the differences or are most affected by forest type?
3. Is it possible to identify indicator species for forest types that can be used in the future to assess the conditions of managed forests?

2. Materials and methods

2.1. Study site

The Białowieża Primeval Forest (52°43' N, 23°50' E; altitudes between 134 and 202 m a.s.l.) is located in northeastern Poland on the Bielsk Plain. Glacial ablation moraines composed of sandy, clayey and loamy textures occupy 75% of the reserve area, with the remaining area composed of organic deposits, primarily peat. The climate of the region is continental with warm summers and cold winters. Total annual precipitation is 641 mm (85% as rainfall); the mean annual temperature is 6.8°C; and an average of 92 days has snow cover. The study was conducted in the Strict Nature Reserve, which is located in the central part of the Białowieża Primeval Forest and encompasses its most valuable old growth forest stands [28].

To consider the entire variability of the Białowieża forests, we investigated all twelve forest types present in the Strict Nature Reserve. Based on the opinion of a geobotanist, we selected the most characteristic examples of the forest types as defined by the Polish classification, which is based on soil fertility and moisture as the two main factors influencing the productive potential of a forest

site. Forest types can be envisioned along a gradient of increasing fertility as follows: conifer, mixed conifer, mixed deciduous and deciduous, and along a gradient of increasing moisture ranging from moderately humid to humid and boggy (Supplement 1). We established three replicates of each forest type (every plot in different location), for a total of 36 study sites (Table 1).

2.2. Sampling methods

Soil samples were collected in June, July, and October 1999 and in May, July, and September 2000. On each sampling date, five samples were taken from each site to a depth of 15 cm with a 5-cm-diameter metal corer; the top litter layer and any ground vegetation were included in the core. Atypical sites, such as fallen and decomposing wood, mushroom pericarps, and places trampled by animals, were avoided. The samples were extracted using a simplified Tullgren apparatus with 25 W light bulbs until they were completely dry (for at least 10 days). Collembola were sorted from the extracts, and species were identified and counted. Springtails were identified under a binocular microscope (50x) and a light microscope (400x) according to Babenko et al. [31], Fjellberg [32,33], Pomorski [34], Bretfeld [35], Potapow [36], Thibaud et al. [37], and Dunger and Schlitt [38]. Reference specimens are kept at the Department of Forest Protection and Ecology at Warsaw University of Life Science.

2.3. Data analyses

To quantify the densities of Collembola, we used only adult specimens because juveniles could not be identified to species. Despite considerable temporal fluctuations among sampling dates for some species, we used the arithmetic mean to analyse the average abundance of species. To characterise Collembola species diversity, we calculated the total number (richness) of species and the inverse Simpson index, $1/\sum p_i^2$ (where p_i is the proportion of species i of the total abundance [39]).

Species were defined as dominant when densities were above a noticeable kink in a rank abundance curve (not shown; threshold: 173.2 individuals $\cdot m^{-2}$; 61.1% of all species were dominants), and only those species were used in the subsequent analyses of assemblage structure (principal component analysis (PCA), cluster methods, linear discriminant analysis (LDA)) and in the GLM of species densities (see below). To reduce the common double-zero problem of assemblage data, the densities of the dominant species were Hellinger transformed [40] (pp. 271ff and 331).

We analysed the effects of forest type on assemblage similarity by computing a PCA (`rda()` in `vegan` 2.3.4) on a covariance matrix of the transformed density data, and NMDS (nonmetric multidimensional scaling) was run as a check of this method, which yielded very similar results (data not shown). Because the number of replicate sites was limited, we refrained from formally testing for differences of assemblage composition among the forest types.

Instead, and to complement the PCA, we identified groups of sites with similar assemblage compositions with an average agglomerative cluster analysis (UPGMA; `hclust()` in `stats` 3.2.3). We found that UPGMA performed the best among a range of candidate hierarchical methods by comparing the original dissimilarity and the cophenetic distance matrices (details not shown). Additionally, two non-hierarchical methods were computed (k-means partitioning and recursive classification trees) that yielded very similar results to the UPGMA. We decided on the number of interpretable clusters (pruning level of the cluster tree) by graphing fusion level values and, because the results were inconclusive, by using the Calinski-Harabasz criterion for selecting an optimal k-means partition (`cascadeKM()` in `vegan` 2.3.4).

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