A MULTISCALE APPROACH TO EVALUATE THE STRUCTURE OF DIVERSITY OF COLLEMBOLA IN BOREO-NEMORAL FORESTS OF THE RUSSIAN PLAIN

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Received: 08.10.2021. Revised: 28.02.2022. Accepted: 13.03.2022.

Collembola is a group of numerous ubiquitous small soil-dwelling arthropods decomposing the plant residues. The study analyses the diversity structure of this group in mesic conditions of coniferous, mixed, and broad-leaved forests. Sample plots were located in three Protected Areas in the Moscow Region (Losiny Ostrov National Park and the Valuyevsky Forest Park) and Smolensk Region (Smolenskoe Poozerye National Park). In total, 70 species of Collembola were registered in the forest litter. Two Collembola species were of Asian origin, namely *Appendisotoma stebayevae* (noted in Europe for the first time) and *Vertagopus asiaticus* (the second record of this species in the study area). The number of species was close to the number of genera, indicating the allochthonous character of the forest fauna of Collembola of the central Russian Plain. A multiscale approach was applied for sampling design. This allowed us to assess the diversity of Collembola at various spatial scales: from 1 m to hundreds of kilometres. The study scheme included two regions, four localities, 12 sample sites, and 36 plots; the latter was 1 m^2 (the smallest area unit). The data analysis was based on the concept of alpha-beta diversity accompanied by the additive partitioning method. The region (the largest area unit) was the most important factor in forming the species diversity. The type of forest litter (coniferous vs. broad-leaved) was less significant; the habitat heterogeneity factor made even a less contribution. On average, 1 m^2 of forest litter comprised about a quarter of the entire list of Collembola species in the studied forests. The species richness of Collembola in the broad-leaved forests was more variable in space and in time compared to coniferous forests and mixed forests; a transitional pattern was observed. The species composition of Collembola varied between the seasons of the year by about a quarter when considering the same sites of coniferous and mixed forests. In broad-leaved forests of various areas, seasonal changes in species composition varied highly, from very pronounced to insignificant. The new concept of plant litter traits is discussed as a factor for affecting the patterns of the structure and dynamics of the Collembola species diversity.

Key words: additive partitioning, alpha-beta-gamma diversity, microarthropods, seasonal dynamics, soil mesofauna, spatial scales, species richness, springtails

Introduction

Biodiversity is affected by a large number of factors; each one operates at a certain spatial scale. At regional level (the largest area unit), these are climatic and geological factors; at microlevel (the smallest one), the main factor may be the distribution of resources or interspecific interactions (Turner, 1989; Azovsky, 2000; Ettema & Wardle, 2002). Regional diversity (γ-diversity) is calculated as the sum of the α- and β-components, where α-diversity is the average number of species on a certain site, β-diversity is the difference of the species lists between the sites. Additive partitioning is applied to study the structure of diversity taking into account the area size, when α- and β-components of diversity are decomposed into the levels corresponding to regions, areas, habitats, and others (Gering & Crist, 2002; Stendera & Johnson, 2005). For example, if α is the number of species in a certain habitat, then β_1 is the difference in species composition between habitats, β_2 between the areas comprising these habitats, and so on.

Much interest is paid to this analysis because a higher or lower contribution of the β-component is usually interpreted as a higher or lower contribution of various factors preconditioning diversity. At the habitat level, this may be the species sorting in regard to abiotic factors, at the regional level, these are geological and historical factors (Leibold et al., 2004; Potapov et al., 2020).

Additive partitioning is currently used in the study of benthic protists and invertebrates (Azovsky et al., 2016), fish (Francisco-Ramos & Arias-González, 2013), bats (Pech-Canche et al., 2011), butterflies (Summerville & Crist, 2003), beetles (Crist et al., 2003), and others. In soil zoology, this method has been first applied relatively recently. The large role of forest microhabitats, including tree trunks, is reported for oribatid mites in Ireland (Bolger et al., 2014). The forest type turns out to be more significant than the microhabitat for testate amoebae in protected forests of the Northern Urals (Tsyganov et al., 2015). Various zones of the forest belt made a great contribution to the diversity of Collembola in protected pine forests of the Russian Plain (Kuznetsova & Saraeva, 2018).

Small ubiquitous soil arthropods, Collembola, are the object of this study. Most experts distinguish them as a separate class of Collembola, which is included together with insects in the Hexapoda superclass of the Arthropoda phylum. Collembola use fungal mycelium and spores as food; they also consume bacterial and algal films, plant pollen, and tissues of living plants (Hopkin, 1997; Potapov et al., 2020). The numerous and diverse Collembola belong to the ecological size group of the soil mesofauna.

Collembola are abundant in the forest litter, which is both their habitat («home») and food resource (Fujii et al., 2020). Coniferous litter decomposes slowly, creating a large space, while broad-leaved litter provides more accessible food resources. Some authors conclude that coniferous forests make a greater contribution to Collembola diversity (Salamon et al., 2008); other habitats considered are broad-leaved forests (Korboulewsky et al., 2021) or mixed forests (Hansen & Coleman, 1998; Ganault et al., 2021).

In coniferous and broad-leaved forests of European Russia, the total diversity of Collembola is about the same order of magnitude, while the local diversity (at the sample level) is lower in broad-leaved forests (Chernov et al., 2010). We assume that the spatial structure of Collembola diversity in these forests varies significantly at different spatial scales. Our study aims to find out the spatial and seasonal structure of Collembola diversity in protected mesic forests (coniferous, mixed, and broad-leaved) in the centre of the Russian Plain.

Material and Methods

The study was carried out in boreo-nemoral forests in the Smolensk Region and Moscow Region (further referred to «regions»), the largest area units in accordance with the terminology adopted in landscape ecology. The distance between these two regions is about 400 km. These territories belong to the Smolensk-Moscow bioregion as part of the Smolensk-Trans-Ural ecoregion (Ogureeva et al., 2004). The climate in the Smolensk Region is generally more humid and warmer than that in the Moscow Region. The average annual temperature in the Moscow Region is +5.8 °C, in the Smolensk Region, +6.1 °C; the average annual precipitation is 678 mm and 773 mm, respectively. The weather conditions in May, the month preceding the sampling performed in early June in both regions, were colder and wetter in Moscow Region than the annual average (2017), but warmer and drier in Smolensk Region (2018) (Online Weather Archive, 2021).

In each region, two forest locations were studied. In Smolensk Region, this was the territory of Smolenskoe Poozerye National Park (UNESCO Biosphere Reserve); the locations were at a 17-km distance (nearby the villages of Petrakovo and Myakury; Fig. 1). In Moscow Region, the study was carried out in the Losiny Ostrov National Park (Losinka; Fig. 1) and the Valuevskiy Lesopark (Protected Green Territory, Valuevo; Fig. 1) distanced for 48 km from each other.

The plots were located on slightly disturbed areas of mature forests: broad-leaved, coniferous (spruce, *Picea abies* (L.) H.Karst.), and mixed (spruce-oak, *Picea abies – Quercus robur* L.) forests. *Tilia cordata* Mill. dominated in broad-leaved forests in all regions; *Carex pilosa* Scop. prevails in the grass layer. In coniferous forests, these were *Picea abies*, *Oxalis acetosella* L., and green mosses. In mixed forests, *Picea abies, Tilia cordata, Quercus robur*, and *Carex pilosa* dominated. Forest types differed also in litter depth, which was 1–3 cm in broad-leaved forests, 3–4 cm in coniferous forests, and 1.5–4.0 cm in mixed forests.

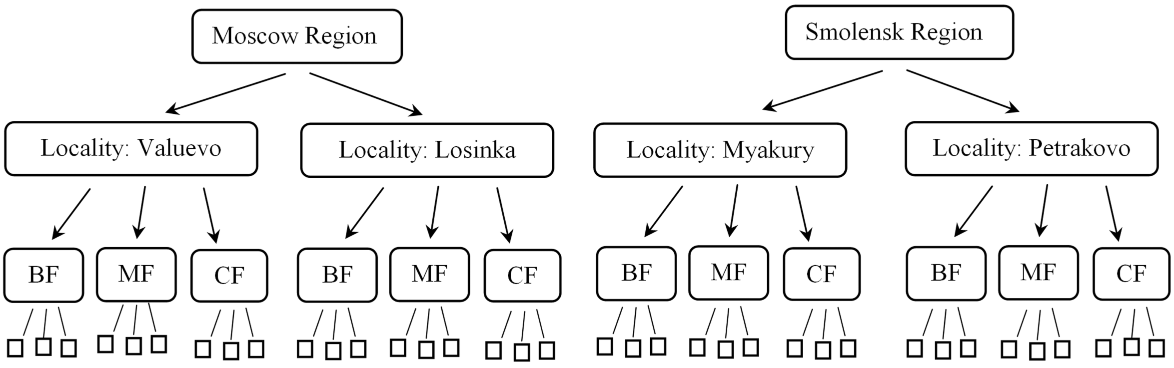

Fig. 1. Sampling design in Protected Areas of the Moscow Region and Smolensk Region. Designations: BF, MF, CF are the sampling plots of broad-leaved, mixed, and coniferous forests, respectively. The squares in the bottom row represent 1-m^2 samples.

In all forest types in each particular region, the censuses were carried out within one day. Each series included 81 samples, which were taken with a soil corer (8-cm^2 sampling diameter). The samples included litter, humus layer, and 1–2 cm of the upper mineral soil layer. The series consisted of three groups of samples taken at a 10-m distance from each other in a relatively homogeneous ground cover of the inter-canopy space. The censuses were quite intensive, since each group included 27 samples within 1 m^2 arranged in a fractal pattern (Marsh & Ewers, 2013). The scheme was described in detail by Vasenkova & Kuznetsova (2019).

Here, we analyse the diversity of Collembola, starting from the level of 1-m^2 plots and moving gradually to the largest area unit (region). In general, the design of the multiscale study included two regions, four locations, 12 sample plots, and 36 plots of 1 m^2 (Fig. 1). In addition, the censuses on sample plots in the Moscow Region were carried out in summer and autumn to assess changes in diversity over time (six series).

Collembola were extracted using Tullgren funnels, fixed with 80% alcohol, mounted in microslides in Phoera liquid, and identified down to the species level, in some cases, down to the genus level (Babenko et al., 1994; Fjellberg, 1998, 2007; Potapov, 2001). Species designated «sp.» in Appendix 1 and Appendix 2 are valid species, but not juveniles of other species. The completeness of assessing the species richness of Collembola was analysed using cumulative curves, which were characterised by an increasing trend in the number of species as the number of samples grew. Matrices of the number of species for individual samples (8 cm^2) of each series were analysed using the Chao2 index in the PAST 3.21 (Hammer et al., 2001). Following the adopted terminology in landscape ecology, here we use the terms «species richness» and «species diversity» (or simply «diversity») as synonyms, despite the well-known difference between them.

The sampling scheme was designed especially in order to reveal the diversity structure of Collembola in various types of the litter in forest ecosystems of the mixed forest subzone in European Russia (γ_{total}). Alpha-diversity (α_m) was set as the average number of species per 1-m^2 plot. Beta-diversity was divided into four levels: region (β_{reg}), location (β_{loc}), site (β_{site}), and intra-site heterogeneity (β_m). In this article, we use «site» when talking about a sampling site in a particular habitat. Analysis was performed using the «adipart» function (Crist et al., 2003) in the «vegan» package of the R software environment (Oksanen et al., 2015). Matrices for calculations combined the data on the number of individuals of each species in particular samples. The results of partitioning reflected the observed share of α-level and each of β-levels of the given sample to the gamma diversity ($\gamma = 1$). Alpha-components were calculated as simple averages (weights = «unif»). The number of species was used as an index (index = «richness»). For each level, the estimates of the significance of the observed values from the expected ones are given at a random distribution of diversity components (nsimul = 5000). The significance level was set as $p < 0.05$. The following equations were used for additive partitioning by spatial scales for samples of different sizes:

$$\gamma_{total} = \alpha_m + \beta_m + \beta_{site} + \beta_{loc} + \beta_{reg} \text{ (total sample);}$$
$$\gamma_{reg} = \alpha_m + \beta_m + \beta_{site} + \beta_{loc} \text{ (for each region);}$$
$$\gamma_{loc} = \alpha_m + \beta_m + \beta_{site} \text{ (for certain location),}$$

where α_m is the average number of species at the 1-m^2 plot; β_m is the difference in the species composition of Collembola within the habitat-site (10 × 10-m area); β_{site} is the difference between the sites; β_{loc} is the difference between locations; β_{reg} is the difference between the regions.

Seasonal sampling at the same sampling plots in Moscow Region (summer and autumn) made it possible to assess the seasonal structure of diversity, i.e. seasonal differences (β_{ss}) according to the following equation:

$$\gamma_{ss} = \alpha_{site} + \beta_{ss} ,$$

where α_{site} is the average number of species at the site; β_{ss} is the difference in species composition between seasons.

In total, 13 229 Collembola from 18 series and 1458 samples were considered. In the Moscow Region, six series of samples were taken at six plots in summer (07.06.2017, and 13.06.2017) and in autumn (30.09.2017, and 02.10.2017). In the Smolensk Region, six series of samples were taken at six plots in summer only (06–07.06.2018). The diversity of the regions was compared only for summer series, seasonal changes were estimated using the material from the Moscow Region only. The dataset analysed in this article was published in the Global Biodiversity Information Facility (GBIF) international information system as two datasets («sampling event» type), comprising 5447 records in total (Vasenkova & Kuznetsova, 2021a,b).

Results

General characteristics

The total abundance of Collembola in the forests differed by an order of magnitude according to summer sampling from 2100 individuals/m^2 (ind./m^2) to 21 400 ind./m^2. In particular, 2100–13 200 ind./m^2 in broad-leaved forests, 4000–14 000 ind./m^2 in mixed forests, and 10 600–21 400 ind./m^2 in coniferous forests. In autumn, the abundance was higher, except for mixed and coniferous forests in Losiny Ostrov National Park. The most numerous species were *Isotomiella minor* (Schäffer, 1896), *Parisotoma notabilis* (Schäffer, 1896), and *Folsomia quadrioculata* (Tullberg, 1871) (Appendix 1, Appendix 2).

In total, 70 species of Collembola were found in the studied forests (Appendix 1, Appendix 2). These were mainly widespread nemoral and eurybiont species, except two unexpected records of Asian Collembola species, *Appendisotoma stebayevae* (Grinbergs, 1962), and *Vertagopus asiaticus* (Potapov, Gulgenova & Babykina, 2016). On average, 23 species per habitat were found in broad-leaved and mixed forests, and 25 species, in coniferous forests (Fig. 2). The ratio of the number of species to the number of genera (S/G) was extremely low, 1.0–1.1 in Moscow Region and 1.1–1.2 in Smolensk Region.

Assessing of the completeness of revealing of the species composition

The species composition of each series was assessed at significant level of 87–99% according to the Chao2 index. The species richness of Collembola varied greatly in the series from broad-leaved forests, but it was relatively constant in coniferous forests, being transitional in mixed forests (Fig. 3).

Additive partitioning of the beta-diversity of Collembola of the total material representing the boreo-nemoral forests of the Russian Plain (γ_{total}=1) was carried out only for summer series. The following contributions of various spatial diversity levels were calculated:

$$\gamma_{total} = 0.25\alpha_m + 0.12\beta_m + 0.18\beta_{site} + 0.13\beta_{loc} + 0.32\beta_{reg}$$

Partitioning results for all diversity levels, except for β_{loc}, differed from random values ($p < 0.01$). On average, 1-m^2 plots of the forest litter (α_m) included a quarter of the number of species inhabiting the studied forests. The pattern structure within the habitat (β_m) had the smallest (0.12), but significant contribution to the total diversity. The proportion of diversity was relatively small (0.18) due to the differences between sites; the contribution of location was random (p = 0.09), and the largest differences were associated at the regional level (β_{reg}).

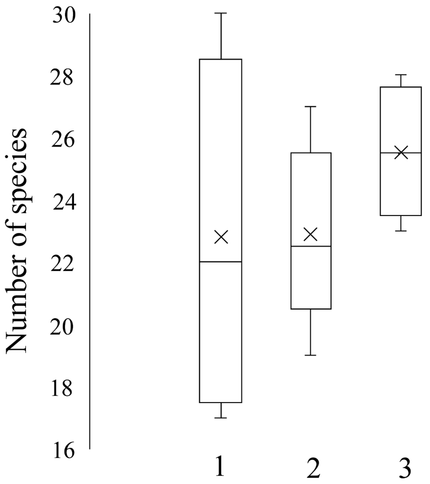

Fig. 2. Average number of species per series in various forest types in the total material. Designations: 1 – broad-leaved forests, 2 – mixed forests, 3 – coniferous forests. The horizontal line in the bar indicates the median; the cross is the arithmetic mean; the upper and lower sides of the bar are the upper and lower quartiles, respectively; the whiskers are the absolute maximum and minimum values of the number of species.

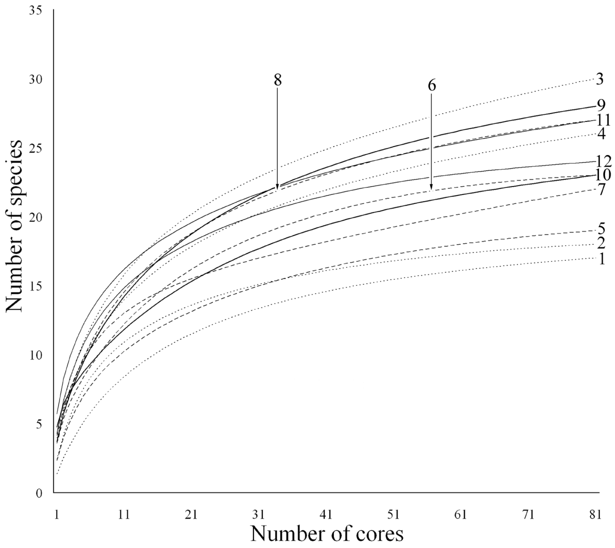

Fig. 3. Accumulation of the number of species in the sampling series depending on the number of cores. Solid lines refer to the series in coniferous forests, shaded lines to the series in mixed forests, dot lines to the series in broad-leaved forests. Sampling series in the Moscow Region are numbered as lines with numbers of 1, 5, 9 (Valuevo), and numbers of 2, 6, 10 (Losinka); in Smolensk Region, as lines with numbers of 3, 7, 11 (Myakury), and numbers of 4, 8, 12 (Petrakovo).

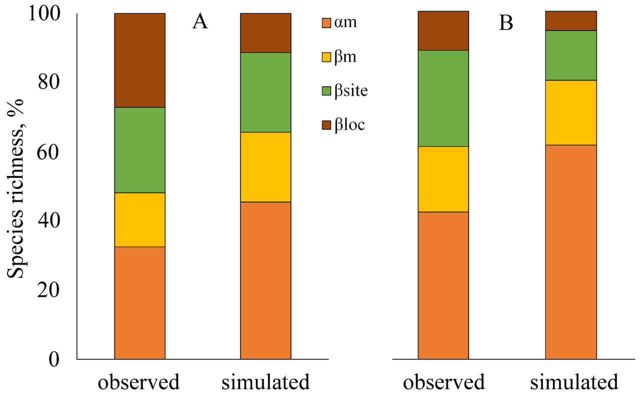

Fig. 4. Additive partitioning of spatial Collembola diversity in the Moscow Region (A) and Smolensk Region (B). Designations: α_m is the average number of species per 1 m^2 of forest litter; β_m is the heterogeneity of areas of the same habitat; β_{site} is the differences between forest types; β_{loc} is the difference between locations of the same region; «observed» indicates *in-situ* data, simulated – the expected data at a random distribution of components.

Diversity partitioning at a lower level, within each region ($\gamma_{reg} = 1$), was significant at all levels ($p < 0.01$), except for β_m in the Smolensk Region and β_{site} in the Moscow Region (Fig. 4). In the Smolensk Poozerye National Park, 42% of the species recorded on average at the smallest area units of 1 m^2 (α_m); in the Moscow Region, the α_m contribution was lower by 10%. In addition, the locations in the Moscow Region differed from each other more than the locations in the Smolensk Region (by 28% and 13%, respectively).

The diversity partitioning at a lower level, within each location ($\gamma_{loc} = 1$), had a high similarity (Table 1). On all locations, on average, 44–49% of the number of species was found at 1-m^2 plots. The differences between plots did not differ statistically from random. The contribution of the forest type to the diversity of Collembola on a certain location was also significant ($p < 0.001$), ranging 31–35%.

Diversity partitioning over time

Seasonal differences in the species composition of Collembola at the same sampling plot were evaluated for the Moscow Region. The proportion of species constantly found in the habitat (regardless of the season) was high by ranging from 71% to 87% (Table 2). In coniferous and mixed forests, seasonal differences were significant and similar in both localities of the Moscow Region (23–24% in coniferous forests and 27–28% in mixed forests). In broad-leaved forests, the contribution of the seasonal factor differed more than twice in different localities: 13% vs. 29%. In all cases, the significance level was $p < 0.001$.

Table 1. Additive partitioning of spatial Collembola diversity within the localities (γ_{loc}) according to data of summer samplings

Locations	Partitioning levels		
	α_m	β_m	β_{site}
Valuevo	0.44^{***}	0.21^{ns}	0.35^{***}
Losinka	0.44^{***}	0.22^{ns}	0.33^{***}
Myakury	0.47^{***}	0.22^{ns}	0.31^{***}
Petrakovo	0.49^{***}	0.20^{ns}	0.31^{***}

Note: α_m is the average number of species per 1 m^2 of forest litter; β_m is the heterogeneity of areas of the same habitat; β_{site} is the differences between forest types; β_{loc} is the difference between locations of the same region. Significance level $p < 0.001$ is designated as ***, insignificant differences as «ns».

Table 2. Additive partitioning of Collembola diversity in time (summer vs. autumn) according to the dataset obtained in the Moscow Region

Series	Partitioning levels	
	α_{site}	β_{ss}
Broad-leaved forests		
Valuevo	0.71^{***}	0.29^{***}
Losinka	0.87^{***}	0.13^{***}
Mixed forests		
Valuevo	0.73^{***}	0.27^{***}
Losinka	0.72^{***}	0.28^{***}
Coniferous forests		
Valuevo	0.76^{***}	0.24^{***}
Losinka	0.77^{***}	0.23^{***}

Note: α_{site} is the average number of species per habitat; β_{ss} is the difference between seasons. Significance level $p < 0.001$ is designated as ***.

Discussion

The species composition of Collembola of European Russia and entire Europe is supplemented by a new species, *Appendisotoma stebayevae*, which has been known to date only from dry steppes of the continental part of Asia (Republic of Tuva, and Republic of Khakassia in Russia; Kazakhstan, Kyrgyzstan, and Mongolia) (Potapov, 2001). In our collections from the Moscow Region, we found *Vertagopus asiaticus*, a nemoral bark-dwelling species, numerous in taiga forests from the Urals to the Russian Far East (Potapov et al., 2016). The second finding of the species in the centre of European Russia suggests the invasive spread of *V. asiaticus* to Europe (Potapov & Janion-Scheepers, 2019).

The average species richness of Collembola in forest ecosystems of the temperate zone is low, 25–30 species per habitat (Petersen & Luxton, 1982; Salamon et al., 2008; Chernov et al., 2010; Russell & Gergócs, 2019). In our samples, this indicator is nearly the same, 23–25 species. Slightly lower indicators in our material are due to the limitation of the sampling areas by only the inter-canopy space, targeting on the greatest comparability of the results from different territories. In this study, we did not examine areas near tree trunks, study of which usually allows adding several species to Collembola diversity.

The actual number of Collembola species in the habitat is higher, since sampling during another season adds from 13% to 29% (on average, 25%) to the species composition of Collembola at the same sampling habitat. If the number of repeated samplings is large, as during long-term studies of Collembola in the oxalis-spruce forest, then the total number of recorded species may exceed 50 (Kuznetsova, 2007). High differences in the population density of common and rare species are the reason for the difficulty in revealing the species composition of Collembola. According to the same dataset, these differences may reach four orders of magnitude if one considers the total material.

The predominant process of the fauna formation in the region may be assessed by the ratio of the number of species to the number of genera (S/G). At a high S/G ratio, it is considered autochthonous, at a low ratio allochthonous. A low ratio (close to 1.0) indicates that each genus is represented by one species due to its migration to the region (Malyshev, 1969; Tolmachev, 1974). In the Moscow Region, this indicator is 1.1 on average, in the Smolensk Region 1.2. This suggests a predominantly allochthonous nature of the formation of the fauna in these regions. Indeed, the centre of European Russia was affected by the Pleistocene glaciations, which mastered the diversity of various taxa, including plants (Markova et al., 2019).

A relative constancy of Collembola species richness in coniferous forests, compared with mixed and, especially, broad-leaved forests is observed in the present study. The reason for this phenomenon seems to be associated with the properties of the forest litter, which are both microhabitat and food source for Collembola. Indeed, the regulation of soil animal communities (including that of Collembola) is bottom-up, i.e. the availability of resources is recognised as more significant than the regulation of populations by predators (Ettema & Wardle, 2002). Recently, the concept of plant litter «traits» has been proposed, offering a quantitative method for analysing the relationship between vegetation cover and soil animals (Fujii et al., 2020). Two groups of litter traits are identified, being related to the nutritional quality and physical parameters of the litter. In broad-leaved forests, the parameters of both resources and litter space vary widely over time. In coniferous forests, the variability of these parameters is minimal (Fujii et al., 2020), which corresponds to the stability of Collembola species richness in forests of this type, confirmed by our results. The similarity of the average number of Collembola species in coniferous and broad-leaved forests may be associated with the balance of pros and cons of litter of various types for Collembola. The litter of broad-leaved forests is more nutritious, but highly variable (HH type), while the litter of coniferous forests is less nutritious, but more stable in physical parameters (LL type) (Fujii et al., 2020).

Despite the importance of forest litter properties, its contribution (β_{site}) to Collembola diversity is inferior to the regional differences in boreo-nemoral forests (β_{reg}). This means that the so-called process of species sorting (Leibold et al., 2004), according to their adaptation to the properties of various types of forest litter, is less significant for the formation of Collembola diversity in the studied set of forest types compared to the regional species list. It is interesting that in pine (*Pinus sylvestris* L.) forests, which differ sharply in terms of humidity (an important factor for Collembola), the habitat type is not a limiting factor (Kuznetsova & Saraeva, 2018). In general, the conclusion on direct dependence of difference in species lists on the distance between the sampling areas has been suggested earlier for various groups of terrestrial and aquatic organisms (Kuznetsova & Saraeva, 2018; Takada et al., 2021).

On average, a quarter of the total diversity of Collembola (17.5 species) was found per each square meter of forest litter in the mesic forests of both regions studied. Regard must be paid to the significant differences in the species composition of Collembola between 1-m^2 plots of the same site, located at only a 10-m distance from each other considering the entire dataset (γ_{total} = 1). This indicates a noticeable heterogeneity in the distribution of Collembola species within the habitat, even on a relatively small sample area of 10 × 10 m with a fairly uniform vegetation cover. This heterogeneity is due to a local increase in the population density of the number of small-sized species, as well as their accidental entry into the samples. An estimate of this effect of 12% means that 8.4 species may be added on average to the number of Collembola species per 1 m^2 if two more such plots will be studied within the sampling site. Therefore, the average number of species at a 100-m^2 plot is 1.5 times higher than on a 1-m^2 plot.

Seasonal changes in the species composition of Collembola (by about 25%) were fairly constant in the studied coniferous and mixed forests of the Moscow Region, as well as in the pine forests of Karelia (Kuznetsova & Saraeva, 2018). However, in broad-leaved forests, the seasonal «renewal» of the species composition may be pronounced to a different extent (Table 2). This is consistent with the variability in the litter properties in the broad-leaved forests (Fujii et al., 2020). The «renewal» of the species composition occurs both as a result of the seasonal growth of populations of small-sized species and as a result of accidental sampling of certain rare species, which lists are quite long for any type of forests. Migration processes from other habitats are mainly limited to a few «winter species» and do not play a significant role in Collembola diversity dynamics during the growing season (Hågvar, 2010).

Conclusions

The Collembola of the boreonemoral forests of the Russian Plain represent a rather diverse, but historically young, postglacial fauna. A large number of hard-to-identify rare species, which are found by chance, complicates the task of studying the spatiotemporal structure of the diversity of Collembola in the forests of the study area. In order to solve this issue, a multiscale approach has been applied in combination with intensive census. The factor of regional specificity contributes the most to the species diversity of Collembola. The second most important factor is related to the forest type (coniferous or broad-leaved) and associated characteristic features of the forest litter. Differences between the locations of the same region may be considered better random than regular. Heterogeneity of the distribution of small species in the space of one habitat also contributes notably to this process. On average, the number of species at 100-m^2 site exceeds that at 1-m^2 site by 1.5 times.

The diversity of Collembola in broad-leaved forests varies considerably in space compared to coniferous forests, characterised by more stable physical parameters of the litter. The species composition of Collembola of a certain habitat «updates» seasonally by about 25% in coniferous and mixed forests. In broad-leaved forests, seasonal changes in species composition are pronounced to a different extent. In general, the diversity of Collembola is characterised by a relative spatial and seasonal stability in coniferous forests and pronounced variability in broad-leaved forests, while in mixed forests, this parameter is intermediate.

Acknowledgments

The authors are grateful to E.V. Tikhonova and A.P. Geraskina (both – Center for Problems of Ecology and Productivity of Forests of RAS, Russia) for their invaluable help in setting the plots and for their geobotanical descriptions. We specially thank the staff of Smolenskoe Poozerye National Park (Russia) for assistance in organising fieldwork. We are also grateful to M.B. Potapov (Moscow Pedagogical State University, Russia) for consulting in species taxonomy, A.K. Saraeva (Forest Research Institute, Karelian Research Center of RAS, Russia) for support in mathematical data analysis, and N.V. Ivanova (Keldysh Institute of Applied Mathematics of RAS, Russia) for assistance in publishing the datasets through GBIF and their subsequent correction. The authors are grateful to four anonymous reviewers for comments that allowed improving the manuscript and to Daria Martynova for providing the English translation.

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Appendix 1. Species composition of springtails and the number of specimens in one sampling series in the studied forests of Moscow Region.

Family, species, index	Valuevo			Losinka		
	BF	MF	CF	BF	MF	CF
Hypogastruridae						
Ceratophysella denticulata (Bagnall, 1941)	1/0					
Willemia denisi (Mills, 1932)		2/0	11/2	7/5	13/2	3/0
Xenylla brevicauda (Tullberg, 1869)			1/2			
Neanuridae						
Anurida sp.					2/0	
Friesea truncata (Cassagnau, 1958)		0/1	27/19	3/0	0/6	197/83
Micranurida pygmaea (Börner, 1901)	0/1		6/10			
Neanura muscorum (Templeton, 1836)		0/2	6/2			
Pseudachorutes dubius (Krausbauer, 1898)	0/1	2/0				1/0
Pseudachorutes parvulus (Börner, 1901)	2/9	1/10	1/6	2/29		2/5
Odontellidae						
Xenyllodes armatus (Axelson, 1903)					5/0	
Onychiuridae						
Oligaphorura absoloni (Börner, 1901)		1/2	23/66		3/7	26/47
Oligaphorura serratotuberculata (Stach, 1933)		0/1				
Oligaphorura sp.			1/0			
Protaphorura boedvarssoni (Pomorski, 1993)	6/31	5/9	16/45	105/38	108/16	4/0
Tullbergiidae						
Mesaphorura sp.	19/9	30/15	87/54	26/44	68/21	208/44
Metaphorura affinis (Börner, 1902)		9/1				
Stenaphorura quadrispina (Börner, 1901)					5/0	
Isotomidae						
Anurophorus laricis (Nicolet, 1842)		0/1	0/1			
**Appendisotoma stebayevae* (Grinbergs, 1962)			0/1			
Desoria sp.					0/87	32/32
Folsomia fimetaria (Linnaeus, 1758)					0/2	
Folsomia manolachei (Bagnall, 1939)	2/17	1/6	2/100			
Folsomia quadrioculata (Tullberg, 1871)	0/2			28/15	28/34	430/328
Isotoma viridis (Bourlet, 1839)	0/4					
Isotomiella minor (Schäffer, 1896)	30/79	84/71	301/209	53/181	220/60	147/118
Parisotoma notabilis (Schäffer, 1896)	28/146	37/223	126/256	9/126	132/168	282/205
Proisotoma minima (Absolon, 1901)	4/0	0/1	7/26		0/2	5/0
**Vertagopus asiaticus* (Potapov, Gulgenova, Babykina, 2016)					1/0	
Tomoceridae						
Pogonognathellus flavescens (Tullberg, 1871)	1/32	3/36	3/30	8/45	3/53	4/15
Tomocerus vulgaris (Tullberg, 1871)	3/20	5/45	0/27	2/11	0/20	1/1

Family, species, index	Valuevo			Losinka		
	BF	MF	CF	BF	MF	CF
Entomobryidae						
Entomobrya nivalis (Linnaeus, 1758)	0/1	0/6	2/2	–	3/0	18/0
Lepidocyrtus lignorum (Fabricius, 1793)	7/93	25/173	14/79	34/80	30/79	1/20
Orchesella flavescens (Bourlet, 1839)	0/1	0/2	0/11	0/10	0/6	0/7
Orchesella sp.					8/0	
Pseudosinella alba (Packard, 1873)		6/34				
Pseudosinella immaculata (Lie–Pettersen, 1896)			0/1			
Pseudosinella zygophora (Schille, 1908)		0/2				
Sminthurididae						
Sphaeridia pumilis (Krausbauer, 1898)	8/0	2/0	1/0	43/8	6/9	5/2
Arrhopalitidae						
Arrhopalites caecus (Tullberg, 1971)				2/5	0/1	1/0
Arrhopalites principalis (Stach, 1945)			3/0			
Katiannidae						
Sminturinus bimaculatus (Axelson, 1902)			4/0			
Sminthurinus trinotatus (Axelson, 1905)			2/0		3/0	3/0
Sminthuridae						
Allacma fusca (Linnæus, 1758)					2/0	3/0
Caprainea marginata (Schött, 1893)	5/0		14/0	11/1	1/3	
Sminthurus sp.				1/0		
Dicyrtomidae						
Dicyrtoma fusca (Lubbock, 1873)	12/0	8/0	4/1	10/0	5/0	1/0
Dicyrtomina minuta (Fabricius, 1783)	3/0	13/0	5/0		5/0	7/0
Ptenothrix atra (Linnæus, 1758)	1/0	4/0	2/0			
Ptenothrix setosa (Krausbauer, 1898)		0/2				
Bourletiellidae						
Deuterosminthurus bicinctus (Koch,1840)			2/0			
Deuterosminthurus pallipes (Bourlet, 1842)			2/0			
Neelidae						
Megalothorax minimus (Willem, 1900)	7/6	23/11	12/4	4/7	7/4	4/6
Neelides sp.	0/1		0/3	1/0		
Number of individuals	139/453	261/664	685/959	349/605	668/580	1385/893
Total abundance, thousands ind./m^2	2.1/7.0	4.0/10.2	10.6/14.8	5.4/9.3	10.3/9.0	21.4/13.8
Number of genera	17/15	18/20	25/24	18/15	22/19	22/14
Number of species	17/17	19/22	28/24	18/15	22/19	23/14
Number of species / number of genera	1.0/1.1	1.0/1.1	1.2/1.0	1.0/1.0	1.0/1.0	1.1/1.0

Note: BF – broad-leaved forests, MF – mixed forests, CF – coniferous forests. Summer data are given left to slash «/», autumn data, right to slash «/»; asterisk (*) indicates new records for European Russia.

Appendix 2. Species composition of springtails and the number of specimens in one sampling series in the studied forests of Smolensk Region.

Family, species, index	Myakury			Petrakovo		
	BF	MF	CF	BF	MF	CF
Hypogastruridae						
Ceratophysella denticulata (Bagnall, 1941)	4			9		
Willemia anophthalma (Börner, 1901)		1			2	4
Willemia denisi (Mills, 1932)	2	8	1		8	12
Xenylla sp.			1		1	4
Neanuridae						
Friesea truncata (Cassagnau, 1958)	4	40	95	2		
Anurida granulata (Agrell, 1943)	1		6	1	1	3
Neanura muscorum (Templeton, 1836)			1		14	
Pseudachorutes dubius (Krausbauer, 1898)	3		5			
Pseudachorutes parvulus (Börner, 1901)		1	2	2	4	7
Odontellidae						
Xenyllodes armatus (Axelson, 1903)	7			4		24
Onychiuridae						
Oligaphorura absoloni (Börner, 1901)	1	39	28	4	10	48
Protaphorura armata (Tullberg, 1869)	16		1	59	25	
Protaphorura bicampata (Gisin, 1956)	54			15	7	
Tullbergiidae						
Mesaphorura sp.	1	13	9	4	2	23
Stenaphorura quadrispina (Börner, 1901)				2		
Isotomidae						
Anurophorus sp.				1		
Desoria divergens (Axelson, 1900)	22	28	121	31	24	
Folsomia quadrioculata (Tullberg, 1871)	208	138	285	143	340	196
Isotomiella minor (Schäffer, 1896)	298	417	423	392	200	405
Parisotoma notabilis (Schäffer, 1896)	56	143	121	41	31	68
Proisotoma minima (Absolon, 1901)		1	1		2	
Pseudanurophorus binoculatus (Kseneman, 1934)	1	4	5			
Tomoceridae						
Pogonognathellus flavescens (Tullberg, 1871)	55	16	34	9	33	11
Entomobryidae						
Lepidocyrtus lignorum (Fabricius, 1793)	4	10	31	72	20	20
Entomobrya corticalis (Nicolet, 1842)		1			1	
Entomobrya marginata (Tullberg, 1871)						3
Entomobrya nivalis (Linnaeus, 1758)	12	3	34	3		3
Entomobrya sp.	1	19	13	4	14	1
Orchesella bifasciata (Bourlet, 1839)	1	1	5	1	15	21
Orchesella flavescens (Bourlet, 1839)	8		2	21	9	5

Family, species, index	Myakury			Petrakovo		
	BF	MF	CF	BF	MF	CF
Sminthurididae						
Sphaeridia pumilis (Krausbauer, 1898)	21	4	10	15	11	15
Arrhopalitidae						
Arrhopalites secundarius (Gisin, 1958)	5				4	
Arrhopalites sp.	10	1		2	3	1
Katiannidae						
Sminthurinus elegans (Fitch, 1862)	5			1	1	
Sminthuridae						
Allacma fusca (Linnæus, 1758)		1	3		2	2
Caprainea marginata (Schött, 1893)	1					1
Lipothrix lubbocki (Tullberg, 1872)						3
Sminthurus viridis (Linnaeus, 1758)			1			
Dicyrtomidae						
Dicyrtoma fusca (Lubbock, 1873)	22		3	1	1	
Neelidae						
Megalothorax minimus (Willem, 1900)	12	16	29	14		45
Neelides sp.	16					
Number of individuals	851	905	1270	853	785	925
Total abundance, thousands ind./m^2	13.1	14.0	19.6	13.2	12.1	14.3
Number of genera	25	18	24	23	23	20
Number of species	29	22	27	26	27	24
Number of species / number of genera	1.2	1.2	1.1	1.1	1.2	1.2

Note: BF – broad-leaved forests, MF – mixed forests, CF – coniferous forests.

МУЛЬТИМАСШТАБНЫЙ ПОДХОД К ОЦЕНКЕ СТРУКТУРЫ РАЗНООБРАЗИЯ КОЛЛЕМБОЛ БОРЕОНЕМОРАЛЬНЫХ ЛЕСОВ РУССКОЙ РАВНИНЫ

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Collembola – многочисленная группа повсеместно распространенных мелких почвенных членистоногих, участвующих в процессах разложения растительных остатков. Работа посвящена анализу структуры разнообразия этой группы в хвойных, смешанных и широколиственных лесах, произрастающих в мезофитных условиях. Пробные площади были расположены на трех особо охраняемых природных территориях (ООПТ) Московской (национальный парк «Лосиный остров», Валуевский лесопарк) и Смоленской (национальный парк «Смоленское Поозерье») областей. Всего в лесной подстилке было обнаружено 70 видов Collembola. Два вида азиатского происхождения: *Appendisotoma stebayevae*, впервые отмеченный для Европы, и *Vertagopus asiaticus*, как вторая находка вида в Европе. Число видов, близкое к числу родов, может быть свидетельством аллохтонного характера лесной фауны Collembola центра Русской равнины. При сборе материала мы использовали мультимасштабный подход, позволяющий оценить разнообразие Collembola на различных пространственных шкалах: от метра до сотен километров. Схема исследования включала два региона, четыре района, 12 пробных площадей и 36 метровых участков. Анализ был основан на концепции альфа-бета разнообразия с применением метода аддитивного парционирования. Было показано, что фактор «Регион» является наиболее важным для формирования видового разнообразия. Тип лесной подстилки (хвойная или широколиственная) был менее значимым, а фактор неоднородности местообитания вносил еще меньший вклад. Один квадратный метр лесной подстилки содержал в среднем четверть всего пула видов ногохвосток изученных лесов. Видовое богатство Collembola в широколиственных лесах более изменчиво в пространстве и во времени по сравнению с хвойными лесами. Смешанные леса занимали промежуточное положение. Сезонный видовой состав Collembola различался примерно на четверть для одного и того же участка хвойного и смешанного леса. В широколиственных лесах различных районов сезонные смены видового состава варьировали от слабых до сильных. Структура и динамика разнообразия Collembola обсуждается с позиций новой концепции трейтов растительной подстилки.

Ключевые слова: аддитивное парционирование, альфа-бета-гамма разнообразие, видовое богатство, микроартроподы, ногохвостки, почвенная мезофауна, пространственные шкалы, сезонная динамика