



## Beta-diversity partitioning approach in soil zoology: A case of Collembola in pine forests

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### ABSTRACT

The paper analyzes the structure of diversity in Collembola – an abundant group of small soil-dwelling arthropods. Collembola were studied in two regions of East European forest subzones: mid-boreal and boreo-nemoral. The study was carried out in ecological series of pine forests arranged along the moisture gradient: moist sphagnum, mesic green moss, and dry lichen types. The study was repeated in three locations of two subzones in different seasons and years. A fractal-based nested design was chosen for sampling. The hierarchical approach enabled taking account of the contributions made to the total collembolan gamma-diversity by lower-scale units: regions representing different forest subzones, locations within a region, sites within a location, as well as within-site patchiness. Each of these units was considered as an individual level of beta-diversity, and its contribution to the region's total collembolan diversity was calculated by additive partitioning.

It was demonstrated that a square meter of the forest floor contained around a third of Collembola species known to inhabit East European pine forests. The structure of springtails diversity corresponds to the beta-type. The largest proportion to the total gamma-diversity was made by subzone-specific collembolan species compositions. The contributions of the location and site scales within the same subzone were equivalent. Analysis of time series showed that around a quarter of the species composition in a habitat is “replaced” across season and year series, in spite of the substantial sampling effort. The dependence of estimates of  $\alpha$ - and  $\beta$ -components of diversity on the number of partitioning levels is discussed.

### 1. Introduction

The scale-dependent approach to species diversity has been advanced by Whittaker (1960, 1975), suggesting considering the diversity of a region (gamma-diversity) as the sum of  $\alpha$  and  $\beta$  components. The inventory or alpha diversity is the number of species in a site. The differentiation or beta diversity measures the difference between sites, is generated by the turnover of species composition, and describes the pattern diversity. The same level of gamma-diversity can be achieved both when alpha-diversity is high and beta-diversity is low, and vice versa. In the first case, the species diversity of individual habitats is high, their species compositions are similar, and the turnover of species composition is minor. In the latter case, the species richness of habitats is low, the species composition is highly habitat-specific, and the turnover of species composition is appreciable.

This area of research has been promoted by the development of methods for scale-specific quantification of alpha and beta diversity components. This approach enables quantification of the contribution to total diversity depending on the shares of certain sites within a

landscape or certain locations within a region, etc. Each level of diversity is considered not as such, but as a component part of the region's diversity. Diversity components can be analyzed similarly on the temporal scale, i.e. by measuring the contribution of, say, seasonal and among-year variations of species lists. The calculations are based on diversity partitioning methods (Lande, 1996; Crist et al., 2003, etc.) which have been actively developing in recent years (review Legendre, 2014).

These methods were used to study the hierarchical structure of taxonomic diversity, revealing which spatial levels mattered the most for diversity conservation. The scale-dependent approach shows that taxonomic groups need in space of different size for supporting of a diversity of their communities. Microhabitats of a forest ecosystem play an important part in maintaining the diversity of small ground-dwelling organisms: mites and testate amoebae (Bolger et al., 2014; Tsyganov et al., 2014). Contrariwise, communities of some mobile insects (ants, butterflies) differ mainly at ecoregion scale, associated with different types of soil and landforms (Summerville et al., 2003; Paknia and Pfeiffer, 2011). Interesting results were obtained from comparisons of

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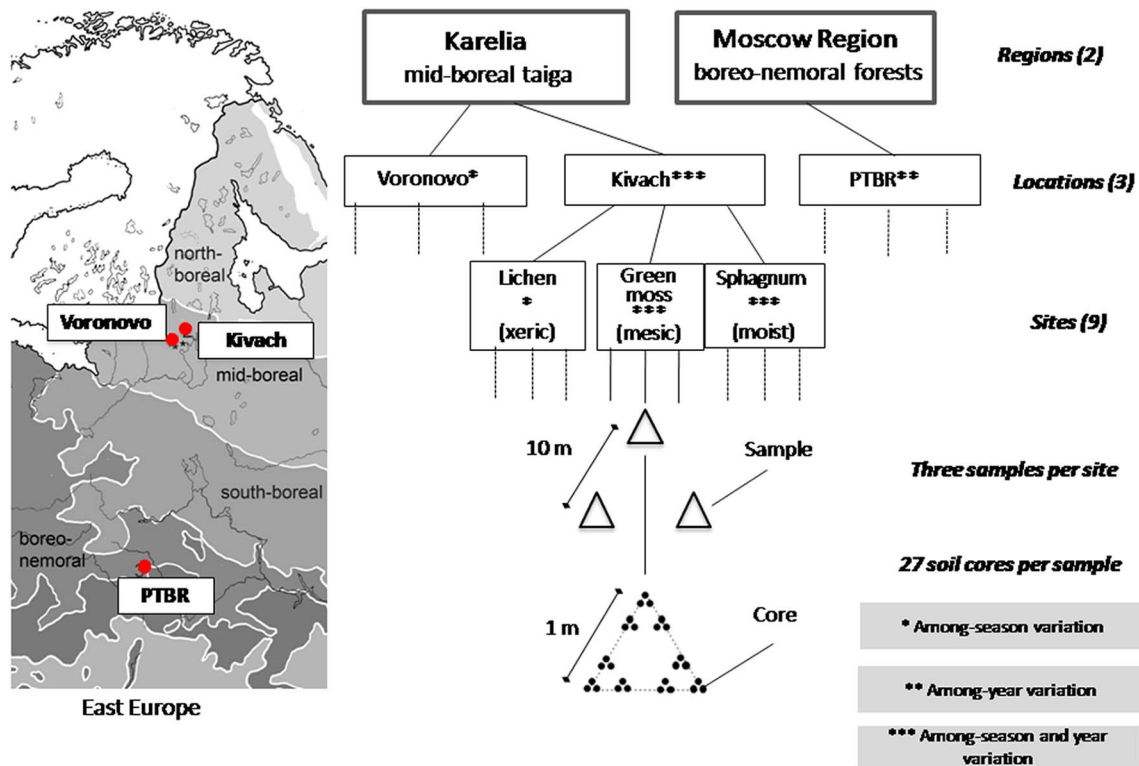


Fig. 1. Map of study locations and hierarchical sampling design.

diversity across spatial and temporal scales. I.e., the variation of the species composition of moth communities among different mountain habitats is not so high as changes of this composition within a year (Highland et al., 2013).

Diversity patterns revealed through partitioning methods derive from constraints on species spatial distribution. Local diversity is currently viewed as arising from a series of filters that species go through in connection with historical processes and environmental factors (Lawton, 1999), as well as from species functional traits that define the feasibility of their life under certain environmental conditions (Violle et al., 2007). Local and regional diversity is constrained by environmental factors and by species dispersal and competition. These filters play different roles in shaping the diversity of the communities of different taxa, generating specific spatial distribution patterns (Leibold et al., 2004).

Like for aboveground organisms, the patterns of biodiversity of ground-dwelling animals are primarily controlled by environmental factors (productivity and disturbance), and are largely similar at the regional scale (Bardgett et al., 2005). The question regarding the similarity of diversity patterns for belowground and aboveground organisms at local scales remains open. One can expect that the structure of the diversity will be influenced by the fact that ground-dwelling communities have more possibilities for niche partitioning in the compact and heterogenous soil environment and for coexistence of a remarkably high number of species at a microscale (Bardgett et al., 2005; Decaëns, 2010). Furthermore, isotopic techniques revealed an unexpectedly wide resource use range and pronounced species-specific trophic specializations in Collembola (Chahartaghi et al., 2005; Potapov et al., 2016).

In spite of all the advances in the partitioning of beta-diversity, these developments are yet to make their way into soil zoology. The diversity of soil organisms has been considered from this angle in Protozoa (Mazei, 2008; Tsyganov et al., 2014) and mites (Bolger et al., 2014). These studies have shown that the micro- and mesofauna of forest soils have different distribution patterns, i.e. a share of  $\alpha$  and  $\beta$

components: in Protozoa the alpha component prevails, at least at the broadest spatial scale, whereas the alpha-diversity in mites is quite low at all scales. This means that there hardly exist any common traits in the diversity structure of soil organisms to discriminate them as a group from above-ground organisms.

As regards the diversity structure of the same group of soil organisms, it was demonstrated that the spatial variability in community composition of Collembola from a pine forest in the Netherlands was closely related to spatial variables (Widenfalk et al., 2016). According to another paper by these authors, the spatial variability was relatively low and did not grow with increasing distance between samples (Berg and Bengtsson, 2007). Overall, the questions raised by Bardgett et al. (2005) about the patterns and determinants of soil biological diversity and even about the very number of soil-dwelling species still remain at the stage of compiling facts and hypotheses (Decaëns, 2010).

The aim of this study was to assess the dependence of Collembola diversity patterns on spatial and temporal scales in pine forests of Eastern Europe. The hierarchical scale in space consists of regions representing different forest subzones, locations within a region, sites within a location, and within-site patchiness. The scale in time includes seasonal and yearly intervals. Collembola, also named springtails, is a numerous and diverse group of microarthropods, whose body length ranges from fractions of a millimeter to several mm. The hypotheses we tested were that: 1) the diversity of Collembola is hierarchically structured at spatial scales from within-site to region and above. This is quite probable given the low mobility of springtails as soil animals and the high number of environmental gradients. Besides, a recent paper about another group of soil mesofauna, mites, demonstrated that  $\beta$  components accounted for at least 50% of the  $\gamma$  diversity at all levels (regional, stand, individual tree and microhabitat scales) in Irish forests (Bolger et al., 2014); 2) differences between coniferous forest subzones (mid-boreal and boreo-nemoral) do not significantly contribute to the diversity of Collembola, since their species composition remains quite similar even for different subzones: the boreal and the nemoral (Chernov et al., 2010), 3) the site level contributes more to the diversity

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