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Analysis of spatial patterns informs community assembly and sampling requirements for Collembola in forest soils

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ABSTRACT

The relative importance of niche separation, non-equilibrial and neutral models of community assembly has been a theme in community ecology for many decades with none appearing to be applicable under all circumstances. In this study, Collembola species abundances were recorded over eleven consecutive years in a spatially explicit grid and used to examine (i) whether observed beta diversity differed from that expected under conditions of neutrality, (ii) whether sampling points differed in their relative contributions to overall beta diversity, and (iii) the number of samples required to provide comparable estimates of species richness across three forest sites. Neutrality could not be rejected for 26 of the forest by year combinations. However, there is a trend toward greater structure in the oldest forest, where beta diversity was greater than predicted by neutrality on five of the eleven sampling dates. The lack of difference in individual- and sample-based rarefaction curves also suggests randomness in the system at this particular scale of investigation. It seems that Collembola communities are not spatially aggregated and assembly is driven primarily by neutral processes particularly in the younger two sites. Whether this finding is due to small sample size or unaccounted for environmental variables cannot be determined. Variability between dates and sites illustrates the potential of drawing incorrect conclusions if data are collected at a single site and a single point in time.

1. Introduction

Populations of most soil fauna have aggregated (patchy) distributions but it is not clear to what extent these aggregations are due to environmental factors, disturbance, intrinsic population processes or stochasticity (Usher, 1969, 1976). Environmental heterogeneity can be related to physical and chemical soil properties, such as soil moisture, temperature, and porosity all of which can cause aggregation (Usher, 1976). Disturbance affects physical and chemical soil properties, resources and their availability (Bardgett, 2002), which in turn, may affect the spatial distribution of organisms (Caruso and Migliorini, 2006; Ettema and Wardle, 2002; Maaβ et al., 2014). Intrinsic population processes, such as dispersal (mainly limitation of), reproduction (e.g. egg clusters, courtship) and competition (exclusion or otherwise) may also affect distribution patterns (Bardgett, 2002; Caruso et al., 2013; Ettema and Wardle, 2002; Hutchinson, 1953; Maaβ et al., 2014; Usher, 1976). In addition to these, there are stochastic elements in the generation of spatial patterns (Hutchinson, 1953) and a large proportion of the observed patterns in soil communities appear to be random (Caruso et al., 2011, 2012).

The mosaic nature of the soil, and the preferences of species for particular microhabitats, potentially restricts competitive exclusion to local patches (within the scale of regular movement of the animals), thereby facilitating species coexistence on a larger scale (Anderson, 1978a). Thus, the spatial and temporal heterogeneity of the soil environment is thought to be a major driver of its biological diversity (Bardgett, 2002). For example, heterogeneity was observed to increase species richness of soil mesofauna in an experiment that manipulated physical soil properties (Nielsen et al., 2010). Similarly, a positive correlation has been found between mite (Oribatida) species diversity and habitat structural complexity (Anderson, 1978b).

The relative contributions of the aforementioned factors to the spatial heterogeneity in the distribution of soil animals are difficult to assess accurately because they do not occur in isolation but are interdependent. For example, the proximal effects of disturbance can be difficult to assess in isolation as they inevitably initiate cascading effects. However, the spatial variation in species composition between sampling points may contribute to our understanding of the maintenance biodiversity (May, 1984; Rosindell et al., 2011). This is particularly relevant in soil, as the 'the enigma of soil animal species

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diversity' (Anderson, 1975) has been, and continues to be, discussed after almost half a century.

While spatial heterogeneity may explain soil species diversity to some extent, it represents a significant practical obstacle to the accurate description of the soil microarthropod community. As most widespread species are found in large numbers and many rare species are not widely distributed, it is inevitable that most species won't occur in all samples unless sample area (Storch et al., 2003) or sampling effort (Chao et al., 2009) are increased. This would require large amounts of money and labour, in particular because the identification of soil microarthropods is time consuming limits the number of samples which can be collected per site (see for example Black et al., 2003; Cole et al., 2008; Deharveng, 1996; Palacios-Vargas et al., 2007; Salmon et al., 2008). Although, random or systematic sampling designs or the combination of sampling techniques (Querner and Bruckner, 2010) may help overcome this to a certain extent, the fact that spatial heterogeneity also affects diversity of species composition (Maaβ et al., 2014; Veech, 2005) poses a challenge in deciphering the number of samples needed to accurately estimate species richness. The analysis of large numbers of samples for a single site over time may help tackle this task.

Neutral theory can be a useful first step when testing for patterns of diversity and abundance. Indeed, in following 'Ockham's razor' philosophy that the model with the fewest assumptions should be preferred, then neutral dynamics can be used at least as a null model in the ongoing investigation into community assembly dynamics (Alonso et al., 2006).

Collembola are one of the most diverse and abundant groups of the soil mesofauna making them ideal candidates for such investigations. They have been used in studies of spatial patterns by Usher (1969) and more recently (Caruso et al., 2009; Sereda et al., 2012). In this study we ask whether community assembly differs from the expected under neutral assembly and investigate the number of samples needed to provide comparable estimates of mean species richness at each site (Caruso et al., 2010; Usher, 1976). Patterns of Collembola at three forest sites of different ages are tested for conformity with expectations of with Hubbell's (2001) neutral model. Neutral theory assumes that communities are assembled by random dispersal, history and chance in a way similar than MacArthur and Wilson's theory of island biogeography (MacArthur and Wilson, 1967). The abundances of each species of Collembola collected over eleven consecutive years in a spatially explicit grid were used to examine (i) whether beta diversity differs from that expected under conditions of neutrality, (ii) whether sampling points differ in their relative contributions to overall beta diversity, and (iii) the number of samples required to estimate the species richness in the forests based on randomised sample, species accumulation curves (sensu Colwell and Coddington, 1994). Given the known links between the diversity of plants and below-ground fauna diversity (De Deyn et al., 2003, 2004; Porazinska et al., 2003; van der Putten et al., 2013; Wardle et al., 1999, 2004) we predict that outcomes will be influenced by the differing ages and structural characteristics of the vegetation at the three sites, with more patchy vegetation leading to a greater beta diversity, (i.e. less random structure), in Collembola communities.

2. Materials and methods

2.1. Site description

The data used are from an eleven year study of the Collembola in three forest sites which are part of the national Long-tern Ecological Research (LTER) network of Latvia (Melecis et al., 2005). The community composition has previously been described by Juceviča and Melecis (2002, 2006), and site characteristics are described in Melecis et al. (1998), see (Table 1) for an overview/summary. Three Scots pine (*Pinus sylvestris* L.) forests of different age (Young, Middle and Old) were investigated in Northern Vidzeme Biosphere Reserve (northern Latvia). The Young site is a 30–40 year old, Middle is a 50–70 year old, and Old site is a 150–200 year old, forest stand. The sites were part of a large scale study to determine whether decreased background pollution burdens were associated with improvements in forest health. These reductions in input were reflected in the soil where the concentrations of nickel and lead reduced from 4.3 to 4.4 to 1.7–2.2 and 41.2–52.0 to 19.6–25.4 mg/kg respectively over the first five years of the study period (Melecis et al., 1998). However, even at their highest, the concentrations of heavy metals were too low to significantly affect Collembola (c.f. Austruy et al., 2016; co-author personal communication).

Table 1
Scots pine forest site characteristics for three forests of differing age, Young (30–40 year old), Middle (50–70 year old), and Old (150–200 year old) site (summarized from Melecis et al., 1998).

Site	Young	Middle	Old
Thickness of O horizon (cm)	6–7	7–8	3–7
pH (KCl)	3.1	2.7	3.2
Tree species and tree stand density (ind./ha)	*Pinus silvestris,* 1131/ha	*P. silvestris,* 537/ha	*P. silvestris,* 181/ha
	Understory: *Picea abies,* 337/ha	Understory: *P. abies,* 100/ha	Understory: *P. abies,* 750/ha
	Betula pendula, 56/ha	*B. pendula,* 25/ha	*B. pendula,* 44/ha
		Juniperus communis, 194/ha	*P. silvestris,* 87/ha
Ground cover plant and moss species (most abundant)	*Vaccinium myrtillus,* *V. vitis-idaea,* *Melampyrum pratense,* *Hylocomium splendens,* *Pleurozium schreberi*	*V. myrtillus,* *V. vitis-idaea,* *M. pratense,* *H. splendens,* *P. schreberi,* *Maianthemum bifolium,* *Ptilium crista-castrensis*	*V. myrtillus,* *V. vitis-idaea,* *M. pratense,* *H. splendens,* *P. schreberi,* *Lerchenfeldia flexuosa,* *Calluna vulgaris,* *Cladonia* spp.
Vegetation pattern	Most uniform		Patchy

2.2. Sampling design

A spatially explicit sampling design was used at three sites. Once a year, for eleven consecutive years (1992–2002), a sampling grid (Fig. 1) comprising 5 parallel 40 m long transects (10 m apart) was laid out at each site and 20 evenly spaced samples (2.5 cm diameter by 10 cm depth) taken along each transect to give a total of 100 samples per date per site. The transects were moved to the right by 0.5 m each year. Samples were transported to the laboratory where Collembola were extracted using a modified high gradient extractor (Juceviča and Melecis, 2002).

2.3. Collembola rarefaction curves

Sample-based and individual-based rarefaction curves were computed for each site and sampling date using 100 randomizations in EstimateS for Windows (version 9, Colwell, 2013). The sample-based curves and their logged versions were used to indicate the number of samples required to provide comparable measures of species richness. The individual-based curve is an estimate of the rate of accumulation in the absence of spatial heterogeneity. If it rises significantly more steeply than the sample-based curve, then the samples are more heterogeneous in species composition than would be expected from sampling error alone. Thus, the difference between the sample-based and the individual-based curves were used to estimate patchiness (Colwell and Coddington, 1994; Gotelli and Colwell, 2001). Significance was tested using 95% confidence intervals (CI). In addition, distributions of individual species were tested for aggregation using the chi-squared test