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Environmental filtering vs. resource-based niche partitioning in diverse soil animal assemblages

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ABSTRACT

Terrestrial invertebrates constitute most of described animal biodiversity and soil is a major reservoir of this diversity. In the classical attempt to understand the processes supporting biodiversity, ecologists are currently seeking to unravel the differential roles of environmental filtering and competition for resources in niche partitioning processes: these processes are in principle distinct although they may act simultaneously, interact at multiple spatial and temporal scales, and are often confounded in studies of soil communities. We used a novel combination of methods based on stable isotopes and trait analysis to resolve these processes in diverse oribatid mite assemblages at spatial scales at which competition for resources could in principle be a major driver. We also used a null model approach based on a general neutral model of beta diversity. A large and significant fraction of community variation was explainable in terms of linear and periodic spatial structures in the distribution of organic C, N and soil structure: species were clearly arranged along an environmental, spatially structured gradient. However, competition related trait differences did not map onto the distances separating species along the environmental gradient and neutral models provided a satisfying approximation of beta diversity patterns. The results represent the first robust evidence that in very diverse soil arthropod assemblages resource-based niche partitioning plays a minor role while environmental filtering remains a fundamental driver of species distribution.

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1. Introduction

The classical view of communities and the assembly processes forming them has historically been dominated by the approaches pioneered by the founders of niche theories. More recently classical theories have been rethought to include stochastic processes such as those related to stochastic demographic fluctuations and dispersal dynamics, which for example are the only mechanisms postulated in neutral theories (Bell, 2001; Hubbell, 2001). Stochastic processes have also been included in the more general framework of metacommunity theories (Leibold et al., 2004; Cottenie, 2005), which focus on the spatial nature of assembly processes and extend the principles of metapopulation dynamics to community ecology. For example, processes such as dispersal

create spatial patterns in species distribution. These spatial patterns do not depend on spatial structure in the distribution of environmental variables although the processes generating these patterns may interact with environmentally driven processes (Smith and Lundholm, 2010). Biotic interaction, too, can create spatial patterns (e.g., segregation of competing species in fairly homogeneous environments), regardless of other spatial processes (Gotelli, 2000; Gotelli et al., 2010). Environmental gradients determine spatial patterns in species distribution by sorting species according to their environmental requirements (e.g., dry-tolerant vs. moist tolerant species) and for a long time community ecology has been synonymous with studying species distributions along such gradients (Morin, 2011).

These various processes are entangled in nature at multiple spatial scales but a key general point we analyse in this paper is that environmental filtering is one component of niche partitioning dynamics, which might or might not involve resource based niche partitioning due to competition for shared resources (Hubbell,

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2005; HilleRisLambers et al., 2012; Adler et al., 2013; Kraft et al., 2014). Interestingly, the point of possible independence of environmental filtering and resource-based niche partitioning has been made both by niche (HilleRisLambers et al., 2012; Kraft et al., 2014) and neutral theorists (Hubbell, 2005) in spite of the fact that several ecologists in practice continue to see niches in the sense of Grinnell, that is to say in terms of species environmental requirements (Chase and Leibold, 2003).

Invertebrates constitute most of animal biodiversity and soil is a major reservoir of this diversity. Soil animal community ecologists, following other animal and plant ecologists (Hubbell, 2001; Dornelas et al., 2006; Ritchie, 2009), for a long time have addressed taxonomically defined assemblages such as oribatid mites, collembolans or nematodes to unravel the mechanisms that allow species coexistence in very diverse systems (Wardle, 2002). Recently, microarthropods have also been investigated within the niche-neutral debates or the more general framework of meta-community theories (Lindo and Winchester, 2009; Nielsen et al., 2010; Caruso et al., 2012; Salmon and Ponge, 2012). However, in recent years studies based on stable isotopes and molecular genetics have clearly shown that assemblages such as oribatid mites or collembolans actually consist of species that can range in diet from being decomposers of low quality organic matter to being top predators of nematodes (Schneider et al., 2004; Heidemann et al., 2011; Maraun et al., 2011). This fact implies a strong bias of previous studies in terms of how observed patterns can inform on underlying mechanisms. For example, if we test neutral theories against niche partitioning theories, we should test these within trophic levels (Hubbell, 2005), which challenges previous studies (Lindo and Winchester, 2009; Nielsen et al., 2010; Caruso et al., 2012; Gao et al., 2014). In general, there is little theoretical and empirical support for the hypothesis that soil animal communities are structured by niche dynamics based on competition (Wardle, 2006; Gao et al., 2014), although several studies have shown that microarthropod communities are sorted by environmental gradients (Auclerc et al., 2009; Lindo and Winchester, 2009; Salmon and Ponge, 2012).

We addressed this general point by focussing on diverse soil oribatid mite assemblages from a dry grassland using a spatially explicit sampling design that allowed us to minimise dispersal processes and focus on environmental filtering and niche partitioning based on food resources. Instead of focussing on taxonomic assemblages, we used the stable isotopes ratios $^{15}\text{N}/^{14}\text{N}$ and $^{13}\text{C}/^{12}\text{C}$, and for the first time focus community analysis on trophic assemblages within which competition for shared resources could be a key process. To further characterise species in terms of traits that can be related to competition for resources, we quantified body size and depth distribution and then defined a trait matrix. We used these data to test the hypothesis that species that were closer in space and time were more dissimilar and vice-versa (limiting similarity concept) than expected by chance. The assumption is that limiting similarity and/or trait trade-offs should be observed if resource based niche partitioning is a mechanism through which species coexist locally while competing for shared resources. Still, resource-based niche partitioning and environmental filtering may act simultaneously. Thus, species could also be sorted along environmental gradients either in relation to the measured traits or not. In fact, environmental filtering and resource-based niche partitioning could also be decoupled if competition is not taking place or is of minor importance. The rationale behind the test of these hypotheses is that demonstrating a clear link between trait differences and environmental distance is a key premise to unravel the mechanisms that allow species coexistence in rich communities (Adler et al., 2013).

2. Materials and methods

2.1. Study area and sampling strategy

This study was conducted in dry grassland in a natural reserve in Mallnow, Lebus (Brandenburg, Germany, 52°27.778' N, 14°29.349' E). This reserve has been managed by low-intensity sheep grazing for at least 500 years and is dominated by *Festuca brevipila* (Poaceae). There are areas where grazing may not occur for one year or longer and plant diversity can be very high locally (e.g., >40 species in a 10 × 10 m plot) although grasses such as *Festuca* spp. dominate the assemblage. In these areas, in April and October 2012 we took soil core samples (local communities) within two undisturbed plots of 15 × 15 m along the slope of a hillside, with the two plots about 20 m apart. The two plots represented spatial replicates of a steep soil textural gradient running from the sandy-loamy soil uphill to highly sandy soil downhill. Main soil parameters such as pH, water content, organic C and N varied along the gradient, in some case with remarkable variation (Supplementary Material, Table S1). Sampling was replicated in the two main seasons (spring and autumn). To standardise the local soil arthropod community, we took soil cores (5 cm diameter, 10 cm deep) centred on the grass *F. brevipila*, which was by far the most abundant species in the area (in some case cover > 70%). Twenty randomly positioned samples per plot were collected in each season (total of 80 local communities) and the position of each sample was recorded in the UTM system.

2.2. Sample processing and analysis

Each soil core was cut into five 2 cm slices to quantify species depth distribution. However, the soil core was the main unit of analysis and we defined the local assemblage as the species inhabiting this unit. Eventually, each species was assigned a depth score based on the weighted average of its depth distribution and depth was treated as a species trait. The soil fauna was extracted in a Macfadyen apparatus for two weeks. All arthropods were preserved in 70% ethanol and the adult oribatids morphologically determined to species level (Weigmann, 2006). Body lengths were measured for each individual under a dissecting microscope (Leica M 165, Wetzlar, Germany) using the software LAS. Each species was assigned a size score based on the average length obtained from a number of replicated measurements (mean number of measurements per species = 85; median number of measurements per species = 30). Soil water content was measured as the difference between the weights of fresh vs. dried soil (soil dry weight, SWD), with samples collected at field capacity. Soil pH was measured in a soil-water suspension, where 3 g of soil and 15 ml distilled H₂O were mixed and stirred. The measurement was conducted in the supernatant until the value remained constant.

Organic carbon (C) and total nitrogen (N) were measured by direct combustion of 30 mg of soil in a Euro EA Element Analyzer (HEKAtech GmbH, Wegberg, Germany). Mean weight diameter (MWD) was calculated as the weighted sum of the proportion of soil particles and aggregates in each size class (2–4 mm, 1–2 mm, 0.5–1 mm and 0.2–0.5 mm), determined by dry sieving of the soil.

2.3. Stable isotope analysis

Specimens were transferred into tin capsules. Rare (e.g. *Carabodes willmanni*) or smaller-sized species (e.g. *Micropoppia minus*) required the pooling of several individuals to reach the biomass necessary to the analysis. After drying at 60 °C for at least 12 h, samples were reweighed and stored in a desiccator until further analysis. The same procedure was used to prepare samples of

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