Relative roles of spatial factors, environmental filtering and biotic interactions in fine-scale structuring of a soil mite community

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ABSTRACT

Community theories suggest that community structuring depends on dispersal limitation, environmental filtering and biotic interactions. However, the relative roles of these factors at fine scale are less well understood. In this study, we attempt to determine the relative roles of spatial factors, environmental filtering and biotic interactions in the fine-scale (5 m) structuring of a soil mite community from a temperate deciduous forest in the Maoershan Ecosystem Research Station in northeastern China. In August 2012, we established three plots and collected 100 samples from each plot in a $5 \times 5 \ m^2$ area using a spatially delimited sampling design. To quantify the relative contributions of the spatial and environmental processes, Moran's eigenvector maps (MEMs), variation partitioning analysis and partial Mantel test were used. Null and neutral models were used to disentangle the effects of biotic interactions. Null mode analyses were conducted for non-random patterns of species co-existence and significant species-pairs in the assemblage of soil mites, and to determine whether the observed pattern was the result of biotic interactions. The neutral model was used to identify whether the community structure shows divergence, convergence or neutrality. The results indicated that the relatively large and significant variance was due to spatial factors in all plots. The contribution of environmental filtering was relatively low and non-significant in all plots based on variation partitioning, while it was significant in Plot II based on a partial Mantel test. Soil organic matter content, soil pH, and soil and litter water content explained a significant part of the variance observed in the distribution of the mite community. Furthermore, the null model revealed a non-random co-occurrence pattern in the soil mite community, and the environmental niche overlap indicated a weak contribution of biotic interactions. The observed mean dissimilarity implied significant divergence in communities based on neutral model analysis. Collectively, these results emphasize that both spatial and environmental processes were important drivers in the fine-scale structuring of soil mite communities in a temperate deciduous forest and that biotic interactions were less influential in the observed pattern.

1. Introduction

Many studies have questioned the manner in which species form assemblages and the rules that govern this process. According to niche and neutral theories in community ecology, the composition of species assemblages can be explained by three processes: dispersal limitation, environmental filtering and biotic interactions (Drake, 1990; Weiher and Keddy, 2001; Gilbert and Lechowicz, 2004; Leibold et al., 2004; Tews et al., 2004). Neutral theories suggest that species are ecologically equivalent and that community structure relies strongly on stochastic processes and dispersal limitation (Hubbell, 2001). In contrast, niche theories emphasize that the appearance of species in a specific habitat is based on biotic interactions and environmental filtering, the latter filtering species from the regional species pool (Diamond, 1975; Chase and Leibold, 2003; Webb et al., 2010). In fact, these

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theories are not mutually exclusive and evidence for both has been reported for various communities at different spatial scales (Lindo and Winchester, 2009; Dumbrell et al., 2010; Caruso et al., 2012b). However, their relative roles are still not well known (Chase and Myers, 2011; Winegardner et al., 2012).

Indeed, the relative roles of spatial factors, environmental filtering and biotic interactions in community structuring are hypothesized to be scale-dependent. Environmental heterogeneity is expected to function at larger scales (Weiher and Keddy, 1995; Swenson et al., 2007; Cavender-Bares et al., 2009; Soberón, 2010), because the substantial variation in environmental variables allows species to co-exist. At larger spatial scales, community structuring may be constrained by spatial factors (dispersal limitation) (Declerck et al., 2011; Sokol et al., 2013; Tang et al., 2013) and dispersal limitation might override environmental filtering in certain habitat types (Bello et al., 2013). In addition, the influence of biotic interactions becomes gradually more important as the spatial scale decreases and they might have no obvious effect at scales larger than small (10^1–10^3 m) or fine (<10^1 m) (Hortal et al., 2010). Moreover, in order to describe the underlying mechanisms of species distribution, it is essential to explicitly consider the variables in multiscales (Hortal et al., 2010). However, processes at the small scale often have been neglected when recognizing processes at large scales and it is difficult to infer that variation at the small scale is regulated by stochastic processes (Anderson et al., 2011). Disentangling the mechanisms at larger spatial scales might be challenging, as insufficient considering underlying processes at relative fine-scales (Anderson et al., 2011; Caruso et al., 2012b).

Soil harbors a large diversity of organisms, which represent most of the world's terrestrial biodiversity (Wardle, 2002; Bardgett, 2005; Bardgett and Wardle, 2010; Decaëns, 2010). However, fundamental questions relating to the causes and maintenance of this diversity remain only partially answered (Bardgett, 2002; Lindo and Winchester, 2009; Ingimarsdóttir et al., 2012; Caruso et al., 2012b, 2013). Environmental variability is known to allow for the spatial co-existence of competing earthworm species, which emphasizes the importance of environmental filtering (Jiménez et al., 2012). On the other hand, Caruso et al. (2013) reported that biotic interactions might be a predominant factor in the structuring of soil metacommunity dynamics. Other publications have also demonstrated the important contributions of biotic competition, environmental filtering, or/and spatial factors to the structuring of soil animal communities (Decaëns et al., 2008; Lindo and Winchester, 2009; Ingimarsdóttir et al., 2012; Caruso et al., 2012b). However, the question of the relative roles of these variables at the fine-scale remains little studied.

Soil mite communities represent ideal assemblages to test the relative roles of the underlying processes in fine-scale community structuring. According to niche theories, environmental heterogeneity can create varied micro-conditions for co-occurring species, whereas environmental conditions seem to be more homogeneous at the fine scale and thus the environmental heterogeneity may be less important in maintaining diverse species at this level. When considering the highly spatial connectivity and reachability, dispersal might be sufficient to allow species to survive in microhabitats with suitable environmental characteristics, in other words, dispersal might be not limiting (Fuentes, 2002). Thus, it may be that spatial factors are not important in regulating community structure at fine scale. Soil mite communities have large diversity at small spatial scales. Given the highly similar resources at the fine-scale, the neighboring coexisting species largely share or compete for limited local resources and spaces (Weiher and Keddy, 1995; Kraft and Ackerly, 2010). Consequently, the biotic interactions have the most opportunity to be a major structuring force at the fine scale (Wardle, 2006; Gómez et al., 2010). However, those

processes may operate simultaneously in a fine-scale community (Logue et al., 2011; Winegardner et al., 2012) and perhaps different in intensity.

In this study we addressed the relative contributions of spatial factors, environmental filtering and biotic interactions on the fine-scale structuring of soil mite communities in a temperate deciduous forest at the Maoershan Ecosystem Research Station in northeastern China. We tested two hypotheses in this study: 1) spatial factors and environmental filtering should play relative minor roles for these communities and 2) biotic interactions should play an important role in community structuring at the fine scale.

2. Materials and methods

2.1. Study site

The study was performed at the Maoershan Ecosystem Research Station ($127°30'$–$34'E$, $45°20'$–$25'N$) of the Northeast Forestry University in Heilongjiang Province, China. This area is covered with typical forests of northeastern China. The region lies within a continental temperate monsoon climate. The climate is characterized by an average annual temperature of 2.8 °C and an average annual precipitation of 884 mm. The average altitude is approximately 300 m and the average degree of slopes is about 10–15°. The type of parent material is granite bedrock and the type of soil is a Hap-Boric Luvisol (Gong et al., 1999). The annual evaporation is approximately 884 mm. The frost-free days are about 120–140.

Soil mite communities were collected in a temperate deciduous forest at the Maoershan Ecosystem Research Station. This location has a 60-yr old secondary forest with an 18 m tall canopy layer. The main tree species include *Fraxinus mandshurica* Rupr., *Ulmus davidiana* Planch. var. *japonica* (Rehd.) Nakai, *Betula platyphylla* Suk., *Populus davidiana* Dode, *Juglans mandshurica* Maxim., *Acer mono* Maxim., *Tilia amurensis* Rupr. and *Populus ussuriensis* Kom., and the main shrub species include *Syringa reticulata* (Blume) Hara var. *amurensis* (Rupr.) Pringle, *Padus racemosa* (Lam.) Gilib., *Acer ginnala* Maxim. and *Corylus mandshurica* Maxim.

2.2. Soil mite communities and soil sampling

Three experimental plot replicates (5×5 m^2) were established at the study site in August 2012. The distance between each replicate (Plot I, Plot II and Plot III) was more than 60 m. Each plot was divided into 100 squares of 0.5×0.5 m^2. Soil mite samples were obtained from the left-bottom area of each square. Square soil samples (15×15 cm^2 and 10 cm depth) were collected for the extraction of mite communities. These communities were removed from 500 ± 5 g of the square soil samples using the Berlese-Tullgren method (Krantz, 1978; Gutiérrez-López et al., 2010), with mites being preserved in a 95% alcohol solution. Adult soil mites were identified to the species level and then were counted respectively (Balogh and Balogh, 1992; Yin et al., 1998; Walter and Proctor, 2001; Krantz and Walter, 2009). Soil mite juveniles were excluded from all analyses (Ingimarsdóttir et al., 2012).

A vegetation-free soil core sample (5×5 cm^2 and 10 cm depth) was taken directly to the right of each square used to sample the soil mites. These soil samples were air-dried and then sieved to 1 mm. To obtain soil's organic matter content, the colorimetric method after digestion in H_2SO_4 was used. The soil water content was determined gravimetrically. In deionized water with a soil/solution ratio of 1:5, the soil pH was obtained (Lao, 1988; Pansu and Gautheyrou, 2003). In addition to the plant species richness (the number of vascular plant species), the DBH (diameter at breast height) and basal diameter of vascular plant, the litter dry weight (10×10 cm^2) and the litter water content were measured.