Original article

The small-scale structure of a soil mite metacommunity

Meixiang Gao [a, b, *], Dong Liu [c], Lin Lin [a, b], Donghui Wu [c, **]

[a] College of Geographical Sciences, Harbin Normal University, Harbin 150025, China
[b] Key Laboratory of Remote Sensing Monitoring of Geographic Environment, College of Heilongjiang Province, Harbin Normal University, Harbin 150025, China
[c] Key Laboratory of Wetland Ecology and Environment, Northeast Institute of Geography and Agroecology, Chinese Academy of Sciences, Changchun 130012, China

ABSTRACT

The metacommunity theory has advanced our understanding of how local communities are structured at multiple scales. However, few studies have addressed the distribution patterns of the metacommunity at a small scale, particularly for those organisms living in belowground ecosystems. Using a combination of the elements of metacommunity structure (EMS) and the null model analyses, the small-scale (50 m) spatial pattern of a soil mite metacommunity was identified in a temperate forest in 2012 and 2013. This study evaluated whether species replace each other across consistent environmental gradients and whether a significant competitive structure exists in the entire community. According to the results of EMS analysis, the soil mite metacommunity showed a Clementsian structure (a grouped distribution of species along environmental gradients), which was significantly correlated with moisture in 2012 and associated with moisture and food resources in 2013. Moreover, the patterns of the soil mite metacommunity were similar in both years. Based on the results of the null model analysis, a non-random co-occurred pattern with more significantly aggregated species pairs and the Pianka's overlap index, which was significantly larger than the randomness model, were detected in each year, indicating a non-competitive community. In conclusion, the study indicated that the environmental filtering with moisture and food resources was an important driver in shaping the soil mite metacommunity into a small-scale Clementsian structure, while interspecific competition was likely not influential.

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1. Introduction

A major task in community ecology is explaining the processes that affect community composition. Several processes have been suggested to illustrate how different species from a regional species pool co-occur locally. Regional processes, such as dispersal limitation, history events and climate change, might function at relatively large scales and control the arrival and colonization of species in local communities. Locally, the community composition may be determined by environmental heterogeneity and biotic interactions. Otherwise, stochastic events (e.g., colonization and extinction) can also take place in large and small scales. However, the relative roles of these underlying processes in the community structures across different spatial scales are still unclear.

The concept of metacommunity, which is defined as a set of local communities connected through dispersal [1], has recently received more attention in community ecology and provided a novel perspective for understanding those processes. Specifically, in community ecology, it is relatively fundamental to disentangle the spatial patterns of metacommunities, as the patterns may promote the understanding of those processes, and, at a minimum, provide approaches for a more detailed examination of the basis of the processes for different patterns [2]. Nevertheless, the spatial patterns of metacommunities are scale-dependent, and the patterns exhibited by a metacommunity might vary at different spatial scales. A few studies have explained the spatial patterns of metacommunities at the local scale (10^3–10^4 m) [3–5]; however, less is known about the spatial patterns of metacommunities at the small scale (10^1–10^3 m) [3]. Moreover, it is necessary to reveal the spatial patterns of metacommunities at different scales within the small scale [6,7], which will provide powers of ascertaining the underlying processes at various scale gradients.

* Corresponding author. College of Geographical Sciences, Harbin Normal University, Harbin 150025, China.
** Corresponding author.
E-mail addresses: gmx102@163.com (M. Gao), liudong@iga.ac.cn (D. Liu), 870807187@qq.com (L. Lin), 825157649@qq.com (D. Wu).

To date, at least six patterns of metacommunities have been identified: nested subsets, checkerboards, Clementsian gradients, Gleasonian gradients, evenly spaced gradients and random patterns [8]. Most studies identifying the six patterns have centered on one pattern at a time, which was usually contrasted with a randomness pattern. Recently, the element of metacommunity structure (EMS) analysis has been suggested an efficient approach to explain the six different patterns. The EMS is also useful for determining whether the observed metacommunity patterns differ from chance occurrences [5], and whether species replace each other across consistent environmental gradients. The EMS analysis relies on three structural elements: coherence, species turnover and species range boundary clumping. The first element (coherence) quantifies the level to which different species are structured and respond to the same environmental gradient. The second element (species turnover) measures the number of species replacements between localities, and a low turnover rate represents a nestedness pattern. The third element (species range boundary clumping) responds to how often multiple species have their range limits in the same sites [9] and allows us to distinguish between Clementsian and Gleasonian patterns. The Clementsian pattern is characterized as groups of species that have similar responses to the environmental variables. The Gleasonian pattern is characterized as a continuum of gradually changing species compositions, where species show individualistic responses to the environment. A combination of the three structural elements enables us to define the structures of metacommunities.

The soil mite metacommunity is selected as a model system, which is one of the numerically dominant microarthropods in temperate forest ecosystems [10]. The soil mite species usually have low dispersal abilities and serve as ideal agents to explain the spatial patterns of a metacommunity at multiple scales [11]. Recently, relative studies have addressed the co-occurring pattern and mechanisms which control the soil mite communities at the small scales or the fine scales ($<10^1$ m) [3]. At a small scale (15 m) in dry grassland, environmental filtering was proposed as a fundamental regulator for species composition, while resource-based niche partitioning was suggested a minor contributor [12]. At a fine scale (5 m) in a temperate forest, spatial and environmental filtering were suggested as important drivers for soil mite assemblages, while the biotic interactions were suggested less influential [13]. However, the information on spatial patterns (the six patterns) of soil mite metacommunity at small scale is still insufficient.

Here, we studied a soil mite metacommunity from a temperate forest in the Northeast, China. Based on a spatially explicit sampling design, we identified the spatial pattern of a soil mite metacommunity at a small scale (50 m) by a combination of the EMS and the null model analyses. This study aims to (1) evaluate the spatial pattern of a soil mite metacommunity at a small scale; (2) determine whether species replace each other across consistent environmental gradients; and (3) test if a significant competitive structure exists in the soil mite metacommunity.

2. Materials and methods

2.1. Description of the 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. The average altitude is approximately 300 m. The parent material is granite bedrock. The soil is Hap-Boric Luvisol [14]. The average slope is approximately 10–15°. The research area is characterized by a continental temperate monsoon climate, which is dry and cold in the winter and warm and humid in the summer. The annual precipitation is approximately 600–800 mm, of which 80% occurs in July and August. The annual evaporation is approximately 884 mm. The mean annual, January and July air temperatures are 2.8 °C, −31 °C and 32 °C, respectively. There are approximately 120–140 frost-free days, with an early and late frost in September and May, respectively.

The soil mite metacommunity was sampled in a temperate deciduous forest at the Maoershan Ecosystem Research Station. The location had an 18-m canopy layer. The sampling site was located within a 60-yr old secondary forest. The dominant tree species were *Ulmus davidiana* var. *japonica*, *Fraxinus mandshurica*, *Betula platyphylla*, *Populus davidiana*, *Juglans mandshurica*, *Acer mono*, *Tilia amurensis* and *Populus ussuriensis*. The dominant shrub species were *Syringa reticulata* var. *amurensis*, *Padus racemosa*, *Acer ginnala* and *Corylus mandshurica*.

2.2. Collecting the soil mite metacommunity and soil samples

One experimental plot (50×50 m^2) was established at the study site in August 2012. The plot was equally divided into 100 squares of 5×5 m^2, with 121 nodes in the plot. Soil samples without a litter layer were collected near nodes, which were located in the left-bottom region of each square. Square (15×15 cm^2 and 10 cm depth) and cylindrical soil cores were sampled using a soil auger (7-cm diameter and 10 cm depth), which were collected to extract the soil mite metacommunity in August in 2012 and 2013, respectively. The soil mite communities were removed from the collected soil samples using the Berlese-Tullgren method [15,16]. The obtained soil mite communities were then preserved in a 95% alcohol solution. All kinds of mites were numbered and identified, only the adult soil mites were identified and counted at the species level [17–20]. Juvenile soil mites were excluded from all analyses [21].

Litter-free soil samples (squares with 5×5 cm^2 and 10 cm depth in 2012, and cylinders with 7-cm diameter and 10 cm depth in 2013) were directly extracted from an area to the right of the location where the soil mite communities were collected. The soil samples were air-dried and sieved to 1 mm. After digestion in H$_2$SO$_4$, the colorimetric method was used to obtain the soil organic matter content (SOM, g kg^{-1}). The soil pH was measured in deionized water with a soil/solution ratio of 1:5. The soil water content (SWC, %) was determined gravimetrically [22,23]. The litter dry weight (LDW, g) and litter water content (LWC, %) were also investigated.

2.3. Statistical analysis

2.3.1. The elements of metacommunity structure analysis

The EMS was used to identify the structure of the soil mite metacommunity in each year. Presence-absence interaction matrices (sites by species) were prepared before performing the EMS analysis (2012 and 2013, respectively). First, the matrices were rearranged using reciprocal averaging (RA, also under the title of correspondence analysis). When focusing on ordering species and sites data along an axis of variation (especially for presence-absence matrix), the RA is considered as the simple and better approach [8]. RA is a simple canonical correspondence analysis based solely on the site by species incidence matrix without environmental variables, which organizes the species with the most similar distributions and sites with the most similar compositions nearest to one another [24]. The reason to select the RA is that the firmest association between soil mite species composition from a sample and spatial distribution of species among samples is represented by the primary axis [5]. Accordingly, when the environmental factors are severely associated with the selected primary axis, those factors would likely be inferred as a significant factor in