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Distinct patterns suggest that assembly processes differ for dominant arthropods in above-ground and below-ground ecosystems

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ABSTRACT

Depiction of the patterns and underlying processes within communities is a key topic in community ecology. However, we still know relatively little about these patterns and processes for the dominant arthropod communities living in above-ground (AG) and below-ground (BG) ecosystems. To test whether the community patterns for AG communities are consistent with those of BG communities and to inform whether the underlying processes are congruous, samples of ground carabid and soil collembolan communities were collected from a primary mixed forest in Northeastern China. Within a 9-ha permanent forest plot, 225 carabid samples were captured using pitfall traps in August 2015, and 768 collembolan samples were collected using soil augers in September 2014. Vegetative, topographic, soil and spatial variables were also measured. Geostatistics, null models and variation partitioning were used to evaluate the spatial distributions, co-occurrence patterns and contributions of environmental and spatial factors, respectively. The carabid community did not show obvious spatial autocorrelation, while the collembolan community showed significant spatial autocorrelation and aggregation on multiple spatial scales. Both communities showed non-random co-occurrence patterns, but of different types. The carabid community was driven by weak and insignificant topographic filtering, while the collembolan community was driven by strong and significant topographic filtering. The two communities were each shaped by spatial factors, but the carabid community's spatial distribution may be regulated by their high dispersal ability, which allowed the beetles to overcome topographic constraints. On the other hand, the collembolan community's spatial distribution may be regulated by their dispersal limitations, which combine with topographic constraints to create an aggregation pattern. Finally, we conclude that the dominant AG and BG arthropod communities exhibit different community structure patterns controlled different spatial processes.

1. Introduction

Explaining the patterns of above-ground (AG) and below-ground (BG) communities and their relationships is an important challenge for understanding how biodiversity is maintained (Hooper et al., 2000). As BG biodiversity is incompletely understood and the patterns of BGs are poorly described, comprehensive comparisons of biodiversity patterns in AG and BG communities are almost entirely lacking (Hooper et al., 2000). However, recognizing patterns and underlying processes of dominant AG and BG communities could provide a proxy for developing approaches for protecting AG and BG biodiversity (Hooper et al., 2000; Wall and Moore, 1999; Wolters et al., 2000). Ground beetles (Carabidae) and soil collembolans (Hexapoda: Collembola) are such dominant communities. They have greater effects on community structure than do others, either because they are dominant or because they are keystone species (Bardgett and Wardle, 2010). Carabids and collembolans are dominant in both abundance and distribution within AG and BG communities in temperate forests, and both groups have spatially structured distributions (Dress et al., 2001). The abundance of both carabid and collembolans is influenced by vegetative, soil and microclimatic factors, but usually with differing intensities (Dress et al., 2001). They also have different dispersal abilities, which might allow

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them to respond differently to spatial and/or environmental constraints. Consequently, ground beetles and soil collembolans are good bioindicators for biodiversity research (Blanchet et al., 2013; Ponge et al., 2003; Rainio and Niemelä, 2003) and suitable study groups for the investigation of community assemblages (Widenfalk, 2014).

It is essential to identify the underlying processes that determine the dominant community patterns for AG and BG ecosystems (Juliane et al., 2013). Ecologists have argued whether or not there are general patterns and processes in community ecology (Lawton, 1999; Roughgarden, 2009; Scheiner and Willig, 2008). Keeping general patterns and underlying processes of the dominant communities in AG and BG implicit can limit the pace and direction of community ecology (Scheiner, 2010; Scheiner and Willig, 2008). Identification of the general connections of patterns and processes among the dominant AG and BG communities improves our understanding of the interactive processes and functions that influence AG and BG ecosystems. Previous studies of underlying processes have mostly addressed ground beetle (Shibuya et al., 2011) and soil collembolan (Caruso et al., 2013) communities. However, few studies have revealed and compared the patterns of these two dominant communities simultaneously in the same habitat and on the same scale. Unfortunately, we still know little about the similarity of such patterns and whether the functions of environmental and spatial factors in assembling the two dominant arthropods communities are congruous. Therefore, in this sutdy, ground beetle and soil collembolan communities were used to conduct test addressing the scientific topics mentioned above.

Partitioning the variation in local community composition into environmental and spatial components provides useful information on important underlying processes (Cottenie, 2005). Environmental heterogeneity regulates community composition and distribution because high heterogeneity theoretically provides more suitable microhabitats and ecological niches for a greater variety of soil faunae. Dispersal capacity is expected to determine the response of a community to the variability of environmental heterogeneity, which would consequently control the distribution and persistence of a community (Cuddington and Hastings, 2004). Scientists have suggested that environmental heterogeneity and spatial factors which to some extent can serve as a dispersal proxy (Heino et al., 2017), simultaneously regulate community assembly, but to varying degrees for different communities (Gao et al., 2014b; Maaß et al., 2015).

The forest litter layer provides a degree of protection to the soil surface by intercepting rain and solar radiation (Putuhena and Cordery, 1996) and buffering the soil surface against fluctuations in soil water content, temperature, and radiation (Sayer, 2006). Thus, temporal and spatial microclimates are relatively more variable in AG than BG (Fekete et al., 2016; Sayer, 2006). Therefore, carabids face relatively high fluctuations in the environmental variables of the ground litter layer, such as temperature, humidity, and solar radiation. Meanwhile, plant richness, abundance, and litterfall properties significantly affect the temperature, humidity, solar radiation and nutrient inputs to the litter layer. Thus, plant variation should strongly affect carabid community distribution and patterns. Adult carabids dwelling in litter layers conduct an unknown portion of their activity in the soil (Lovei and Sunderland, 1996) and may have relatively less interaction with soil factors. Moreover, topographic factors indirectly affect the redistributions of plant and soil variables, and they are suggested to exert a relatively minor influence on ground carabids. Furthermore, carabids exhibit relatively high dispersal abilities at the local scale (Jopp and Reuter, 2005) compared to collembolans. This dispersal ability allows carabids to avoid unfavorable habitats, actively select microhabitats, and arrive at preferable habitats in response to the plant mosaic (Bertrand et al., 2016), with respect to food supply (Bryan and Wratten, 2010; Marrec et al., 2014), anti-predator strategy (Bonacci et al., 2011) and the need for shelter (Bonacci et al., 2004). Thus, non-random aggregation and temporal stability have been reported for carabids in the field (Bonacci et al., 2004; Thomas et al., 2001). Therefore, we would generally expect vegetation factors to be more important than soil and topographic factors for carabids because their high dispersal abilities may allow them to overcome environmental constraints.

Collembolans often exhibit significant changes in species composition along environmental gradients (Ponge and Salmon, 2013). Soil collembolans dwell in the soil and interact directly with soil parameters, and they are obviously affected by soil moisture (Huhta and Ojala, 2006), pH (Dijk et al., 2009), temperature (Rendoš et al., 2016), soil organic matter (Potapov et al., 2017), and substrate quality (Krab et al., 2010; Rantalainen et al., 2004). For example, collembolans are especially sensitive to subtle changes in soil moisture (Kærsgaard et al., 2004) and temperature (Jucevica and Melecis, 2006; Krab et al., 2010). Therefore, we expected that soil factors strongly affect collembolan community distribution and patterns. Vegetation and topographic factors usually serve as indirect factors by changing soil moisture and food supply (Dress et al., 2001; Widenfalk et al., 2015). Thus, we expected that vegetative and topographic factors are less important than the soil variables for collembolan distribution. Although ground collembolans crawl very actively in soil and on wood surfaces on a local scale (Chen, 2013), collembolans dwelling in soil pores are relatively less mobile (Querner et al., 2013). Moreover, most collembolan species disperse more slowly and less efficiently than most carabids at the spatial and temporal scales analyzed in this study. Consequently, low dispersal ability may result in the greater restriction of collembolans due to complicated soil structures. Therefore, we assumed that soil factors are more important than vegetative and topographic factors in shaping soil collembolan communities and that dispersal limitations may regulates the spatial aggregation of these communities.

In this study, we focused on boreal ground carabid and soil collembolan communities in a primary mixed broadleaved-Korean pine forest in China because ground carabids and soil collembolans are diverse and abundant (Gu et al., 2014; Miao and Yin, 2005) and have been identified as good bioindicators in the forest (Cassagne et al., 2006; Kotze et al., 2011; Rainio and Niemelä, 2003). The primary mixed broadleaved-Korean pine forest is a zonal climax vegetation in northeastern mountainous area of China (Chen et al., 2010), and research on its biodiversity is an important contribution for global biodiversity maintenance (Guo and Wang, 2005). Unfortunately, this forest-type zone has been fragmented by over-exploitation. Therefore, understanding the patterns and underlying processes of the two dominant arthropod communities can contribute to the maintenance and recovery of biodiversity. We conducted this study to identify the patterns and the roles of environmental and spatial factors in community assemblages of ground carabids and soil collembolans. We hypothesized that (i) carabid and collembolan communities display aggregation patterns; (ii) carabid communities are more influenced by vegetative factors, less influenced by soil and topographic factors, and regulated by spatial factors characterized by a high dispersal ability; and (iii) soil collembolan communities are more influenced by soil factors than by vegetative and topographic factors and are controlled by spatial factors characterized by dispersal limitations. We expected that carabid and collembolan communities would exhibit similar non-random aggregation patterns that do not support substantial roles of spatial and environmental factors in community structuring.

2. Material and methods

2.1. Study area and experimental plot

This study was performed in a primary mixed broadleaved-Korean pine (*Pinus koraiensis*) forest, which is characteristic of the zonal climax vegetation in Heilongjiang Province of Northeastern China. The experimental plot was located in the Liangshui National Reserve (47°7′-47°14′ N, 128°48′-128°55′ E). The average altitude of the reserve varies from 280 m to 707 m. The reserve has a continental monsoon climate, with a mean annual temperature of -0.3 °C and a mean annual