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Shifting mechanisms of elevational diversity and biomass patterns in soil invertebrates at treeline

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ABSTRACT

Ecologists and biogeographers have long been interested in the underlying mechanisms shaping the elevational patterns of biodiversity. However, most of these studies have been conducted aboveground. Although they deliver key ecosystem functions and services, the elevational diversity and biomass patterns of soil invertebrates, including a wide range of taxa, have been severely understudied, especially at treeline. To address this critical gap, we identified richness, abundance, and biomass patterns of soil invertebrates across an elevational gradient under below-treeline forest (from 1020 to 1770 asl) and above-treeline meadow (from 1790 to 2280 asl), respectively. We aimed to (1) identify the elevational patterns of richness, abundance, and biomass in soil invertebrates across the treeline; and (2) test whether these patterns break and the underlying mechanisms shift at the treeline. We found that both the diversity and biomass of litter-dwelling invertebrates showed hump-shaped patterns below the treeline and monotonically decreasing patterns above the treeline, respectively. Richness association of litter-dwelling invertebrates and herbaceous plants shifted from negative to positive at the treeline. For the soil-dwelling invertebrates, no elevational trends were detected in forest while the diversity decreased monotonically with elevation in meadow. In contrast to basal area and litter thickness in forest, temperature was most strongly related to the diversity of litter-dwelling invertebrates in meadow. We showed the breaks in elevational diversity patterns of soil invertebrates at the treeline, while elevational patterns of biomass did not change. Microclimate replaced productivity as the most important factor driving the diversity patterns of litter-dwelling invertebrates across the treeline with vegetation shifts induced by increasing elevation.

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1. Introduction

The underlying mechanisms shaping the elevational biodiversity patterns and the functioning of ecosystems have long been a central focus of ecologists and biogeographers (von Humboldt, 1849; Nogues-Bravo et al., 2008). Elevational patterns of diversity have been extensively researched across a wide array of taxonomic groups in aboveground organisms, including trees, mammals, birds, reptiles, insects, and amphibians (Rahbek, 2005). However, elevational diversity patterns of belowground organisms, which often represent decomposer subsystems, have been severely understudied (Loranger et al., 2001; Decaëns, 2010), especially those of soil invertebrates. In addition, compared with frequent assessments of species richness variation along elevational changes, elevational patterns for abundance and biomass have been studied less frequently.

Soil animals are essential mediators of multiple ecosystem functions and services, such as decomposition and nutrient cycling (Bardgett and van der Putten, 2014; Wall et al., 2015). Due to the laborious and time-consuming nature of sampling and identification (Decaëns, 2010), the few studies that have explored the elevational diversity of soil invertebrates have mostly concentrated on a focal group representing only a small part of the soil food web, and have generated mixed results. For example, no pattern in dipterans, decreasing pattern in termites, a hump-shaped pattern in beetle families richness (Collins, 1980), and even an increasing pattern in earthworm species richness (Gonzalez et al., 2007) have

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all been reported. To date, the elevational diversity patterns of soil invertebrates across a broad range of taxa remain largely unknown, especially when the vegetation shifts at treelines.

Treelines are among the most striking terrestrial vegetation boundaries separating largely contrasting ecosystems, where forests give way to lower-stature vegetation along a relatively short elevational gradient (Hoch and Korner, 2012). Overall productivity and shifts in biomass allocation between aboveground and belowground occur at treelines in a discontinuous way (Dawes et al., 2015). This characteristic may have knock-on effects on soil communities since above- and below-ground communities interact intimately (Wardle et al., 2004a). However, the effects of changing vegetation characteristics across treelines on the belowground subsystem are poorly understood.

Several mechanisms may govern the elevational patterns of soil invertebrate communities, including microclimatic, productivity, resource heterogeneity and soil property (Werenkraut and Ruggiero, 2014). Mircrolimatic hypotheses supposed that abiotic conditions shape the distributions of species, inducing that fewer species exist at high elevations due harsh conditions compare to low elevations (Grytnes and Mccain, 2007). Productivity hypotheses suggest that species distributions are constrained by total food resource availability (Evans et al., 2005; Hurlbert and Stegen, 2014). Heterogeneity hypotheses suggest that species distributions are controlled by the heterogeneity of differential resources quality (Werenkraut and Ruggiero, 2014). Finally, soil property hypotheses emphasize physical structure, heterogeneity of the soil habitat, and the availability of nutrients may affect the distribution of soil invertebrates (Nielsen et al., 2008). However, whether the mechanisms that drive elevational patterns of the decomposer assemblages shift under different vegetation types above and below the treeline remain unknown.

To address this critical knowledge gap, we chose an oak-dominated forest transect (from 1020 to 1770 asl) that shifts to a meadow gradient (from 1790 to 2280 asl) up to the mountain top as a model system for investigating changes in soil invertebrate communities due to: (1) the strong contrast in terms of vegetation characteristics and plant functional groups between these habitats (Chen and Huang, 1997), and (2) the representative of both habitats across a large climatic gradient. We assessed richness, abundance, and biomass patterns of soil invertebrates across an elevation gradient under below-treeline forest and above-treeline meadow, respectively. We quantified litter-dwelling and soil-dwelling invertebrates separately, based on the different habitats in which they are mainly active. In particular, we tested (i) whether soil invertebrates show an elevational pattern in diversity (richness, abundance) and function (biomass), (ii) whether such a pattern, if it exists, breaks along with the succession from below-treeline forest to above-treeline meadow with increasing elevation, and (iii) whether the underlying mechanisms accounting for the variation in soil invertebrate communities shift at treeline.

2. Materials and methods

2.1. Study system

We selected the Beijing Forest Ecosystem Research Station of the Chinese Academy of Sciences (40°00′-40°03′N and 115°26′-115°30′E), which is located on Dongling Mountain, about 100 km northwest of Beijing city, China, as the study area. The study area has a typical warm temperate continental monsoon climate with an average annual precipitation of 500–650 mm and a mean annual temperature of 5–10 °C. The main soil type of this area is brown soil. The zonal vegetation of montane forest is highly heterogeneous and mainly includes oaks (*Quercus* spp.), mixed species (e.g., *Tilia* spp., *Ulmus* spp., *Acer* spp., *Juglans mandshurica*, and *Fraxinus rhynchophylla*, among others), birches (*Betula* spp.), and poplar (*Populus davidiana*). The forest also includes some conifers and shrubs (e.g., *Larix principis-rupprechtii*, *Pinus tabuliformis, Prunus* spp., *Vitex negundo* var. *heterophylla*, among others). The dominant species of subalpine meadow mainly include *Saussurea purpurascens*, *Carex capillaris*, and *Iris ruthenicar*.

In order to minimize heterogeneity among forest types, ten transects, all of which were dominated by *Q. liaotungensis*, were set up from the base to the top of every mountain western slope (the 10 transects each occupied a different elevational segment of the slopes), so together they formed a single montane forest elevational gradient (1020 m-1770 m). The lengths of the 10-m-wide transects ranged from 80 m to 180 m. Each transect was divided into 10 × 10 m plots (parallel to the slope), resulting in a total of 119 plots in the forest (one plot at one elevation). Above the treeline, 21 plots (10 m × 10 m) with elevational intervals of approximately 20 m along the mountain western slope were also chosen to form an elevational gradient of subalpine meadow ranging from 1790 to 2280 m (which was close to the summit of the Dongling Mountain at 2303 m). Thus, 140 plots across the elevational gradient of forest and subalpine meadow were selected for the study. Each plot was chosen with approximately the same aspect (western slope) and similar slopes (between 22° and 48°), so as to ensure that climate serves as the major abiotic driver varying with elevation in this system. The elevation, latitude, and longitude of each plot were logged by a GPS unit. We enumerated tree and shrub diversity in the mountain forest transect plots. Herb diversity was investigated, and soil animals were sampled in three 1 m × 1 m subplots of each plot both in the forest and in the meadow.

2.2. Plant investigation

In each plot, tree species (DBH ≥ 2.0 cm) were identified. The diameter at breast height (DBH), crown diameter, and height in the tree layer were measured for all individuals. Each species in the shrub layer was identified, and its coverage and height were measured. Three subplots (1 m × 1 m) were mechanically selected (along the diagonal line of each plot) for investigating the abundance, coverage, and height of each herbaceous species.

2.3. Soil animal collection and identification

In August 2013, we applied two methods to sample soil animals in each subplot: (1) All the leaf litter in a 0.6 × 0.6 m quadrat was collected from the OL horizon and the humus layer (OF and OH horizons) to extract litter-dwelling invertebrates. (2) Below the OH horizons, two soil cores with a diameter of 8 cm were sampled to extract soil-dwelling invertebrates. Each sample was placed in a cotton bag to ensure the activity of animals remained unaffected and was sealed to avoid exposure to light prior to extraction by heat in modified Tullgren extractors (Wallwork, 1976). Three litter samples in the same plot were mixed into one sample, and six soil cores were mixed into one sample. Most invertebrates were identified to the family or morphospecies level, aside from Mesostigmata and Prostigmata, which were identified at a suborder level. We recorded the litter-dwelling and soil-dwelling taxa as well as the abundance of invertebrates in each plot. We randomly measured the body length of 10 individuals or of all the individuals when less than 10 were found in one family or morphospecies in each sample. The dry weight (mg) of each individual was calculated based on mass-length regressions (Xu et al., 2015), after which the average body mass of each family or morphospecies in each sample was obtained. Along with the abundance data, we determined the biomass of each family or morphospecies in each sample. The

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