Science of the Total Environment 633 (2018) 529–538

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Environmental correlates underlying elevational richness, abundance, and biomass patterns of multi-feeding guilds in litter invertebrates across the treeline

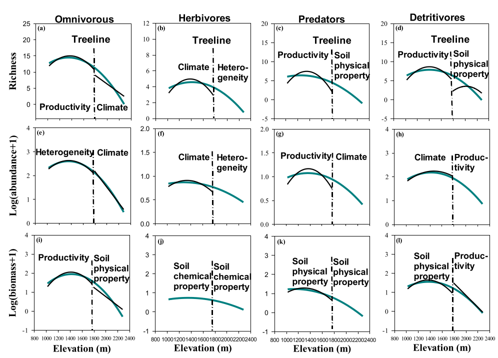
Guorui Xu [a,b], Shuang Zhang [b], Yuxin Zhang [b], Keming Ma [b,*]

[a] Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Menglun, Yunnan 666303, China
[b] State Key Laboratory of Urban and Regional Ecology, Research Center for Eco-Environmental Sciences, Chinese Academy of Sciences, Beijing 100085, China

HIGHLIGHTS

- Elevational patterns of feeding guilds in litter fauna and underlying mechanisms were unclear.
- Detritivores showed a repeated hump-shaped richness pattern above treeline.
- Richness and abundance associations across feeding guilds were ecosystem dependent.
- Biomass of herbivores/predators were related to soil chemical/physical property.
- Underlying environmental correlates shifted at treeline for most feeding guilds.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:
Received 3 December 2017
Received in revised form 18 March 2018
Accepted 18 March 2018
Available online xxxx

Editor: P Elena Paoletti

Keywords:
Altitude
Elevational biodiversity patterns
Environmental correlates
Functional groups
Litter fauna
Treeline

ABSTRACT

Elevational richness patterns and underlying environmental correlates have contributed greatly to a range of general theories of biodiversity. However, the mechanisms underlying elevational abundance and biomass patterns across several trophic levels in belowground food webs remain largely unknown. In this study, we aimed to disentangle the relationships between the elevational patterns of different trophic levels of litter invertebrates and their underlying environmental correlates for two contrasting ecosystems separated by the treeline. We sampled 119 plots from 1020 to 1770 asl in forest and 21 plots from 1790 to 2280 asl in meadow on Dongling Mountain, northwest of Beijing, China. Four functional guilds were divided based on feeding regime: omnivores, herbivores, predators, and detritivores. We used eigenvector-based spatial filters to account for spatial autocorrelation and multi-model selection to determine the best environmental correlates for the community attributes of the different feeding guilds. The results showed that the richness, abundance and biomass of omnivores declined with increasing elevation in the meadow, whereas there was a hump-shaped richness pattern for detritivores. The richness and abundance of different feeding guilds were positively correlated in the forest, while not in the meadow. In the forest, the variances of richness in omnivores, predators, and detritivores were mostly correlated with litter thickness, with omnivores being best explained by mean annual temperature in the meadow. In conclusion, hump-shaped elevational richness, abundance and biomass patterns driven by the forest gradient below the treeline existed in all feeding guilds of litter invertebrates. Climate replaced productivity as the primary factor that drove the richness patterns of omnivores above the treeline, whereas heterogeneity replaced climate for herbivores. Our results highlight that the correlated elevational richness, abundance, and

* Corresponding author at: Research Center for Eco-Environmental Sciences, Chinese Academy of Sciences, Beijing, No. 18 in Shuangqing Road, 100085, China.
E-mail address: mkm@rcees.ac.cn (K. Ma).

https://doi.org/10.1016/j.scitotenv.2018.03.212

biomass patterns of feeding guilds are ecosystem-dependent and that the underlying environmental correlates shifted at the treeline for most feeding guilds.

1. Introduction

Elevational biodiversity patterns and underlying mechanisms have evoked the strong interests of ecologists for centuries (Sundqvist et al., 2013). Considered to be a substitute system for studying the consequences of environmental changes on organisms, analyses of the effects of elevational gradients on diversity contribute to the development and evaluation of a range of general theories of biodiversity (Grytnes and Mccain, 2007). Previous studies have primarily investigated the elevational richness patterns (Beck et al., 2017; Werenkraut and Ruggiero, 2011), whereas the elevational patterns of abundance and biomass have been less studied. Essentially, richness is an index based on presence–absence data, and ecologists will gain more information on community structure by analyzing either abundance or biomass. Moreover, most work on biological communities goes beyond examining diversity per se and focuses on how diversity relates to ecosystem processes and function (Saint-Germain et al., 2007). Ecological processes are mostly driven by individuals and their abundances (Roder et al., 2017). Despite high abundance making small invertebrates pivotal in food webs (Hooper et al., 2005), the abundance distributions of invertebrates along elevational gradients remain poorly documented. A limited number of previous studies on the abundance of arthropods have found diverse results: declining (Lee et al., 2012), hump-shaped (Werenkraut and Ruggiero, 2014) or even increasing patterns (Mccoy, 1990) with increasing elevation have been reported. Biomass should be used in community analyses that involve strong functional components (Saint-Germain et al., 2007), especially for terrestrial food webs. As a significant indicator of community structure, biomass is a key variable that indicates productivity, energy flow, and food-web dynamics (Brown et al., 2004). However, we still have limited knowledge on the elevational patterns of invertebrate richness compared with abundance and biomass data (but see Xu et al., 2017), particularly in the perspective of food web structures.

Food webs depict distribution patterns of feeding links across populations through which energy flows from the primary producers (autotrophs) to the top predators in a community (Thompson et al., 2012). As one of the most complex food webs, the soil food web plays a pivotal role in carbon sequestration, nutrient cycling (Bardgett and van der Putten, 2014) and the maintenance of soil health (Wall et al., 2015). Few other biota can match the abundance, diversity or complexity of the soil animals (Bardgett and van der Putten, 2014). The complex feeding links that involve enormous biodiversity (McCann, 2007) in heterogeneous soil habitats (Wardle, 2006) make soil food webs difficult to understand (Van der Putten et al., 2001). Therefore, guilds, functional groups or functional types have been regarded as a potentially useful way to reduce complexity in soil food web research when the effects of environmental changes on biotic communities are investigated (Kissling et al., 2012).

A feeding guild is a group of species that exploit the same resource in a similar way (Root, 1966) and that determines the effects of species on ecological processes and their sensitivity to environmental change (Mumme et al., 2015), which in turn influences the growth, reproduction and survival of a species (Moretti et al., 2016). Moreover, feeding guilds can be considered good surrogates for the trophic level and position in a food web, important components that shape the structure of ecological networks (Ibanez, 2012; Stang et al., 2009), and have a direct link to ecosystem functions. Several studies have shown that the response to environmental change among species in the same feeding guild is often concordant (Crotty et al., 2014; Hillstrom and Lindroth, 2008; Voigt et al., 2003). There are a few studies that have differentiated feeding guilds of soil invertebrates (most concentrating on nematodes) in different environmental contexts. For example, herbivores benefit from low-nitrogen soil, whereas predators and omnivores benefit high-nitrogen soil with increasing CO_2 concentration (Hoeksema et al., 2000). The richness of herbivores (Woodcock and Pywell, 2010) and predators (Haddad et al., 2009) are negatively correlated with plant species. Most elevational studies have focused on a single trophic level or guild, rather than examining patterns for biotic communities across all trophic levels (Wang et al., 2011). Although some studies have reported elevational patterns across trophic levels (Grytnes et al., 2006), few studies have quantified the elevational richness, abundance, and biomass patterns of different trophic levels (often represented by feeding guilds) in soil food webs, especially when contrasting ecosystems separated by treelines.

The relationships between richness and elevation greatly vary with scale of extent (Nogues-Bravo et al., 2008). If the sampling gradients only cover a part of the local elevational range, the outcome of elevational biodiversity studies will be diverse or even misleading. Therefore, to reduce the scale effect on the outcome of elevational biodiversity studies, samplings should cover as much as possible of the entire range of a mountain from base to top, and many elevational gradients should thus contain the treelines in montane areas. Treelines represent drastic vegetation changes where forests are replaced by shrublands or grasslands along a relatively short spatial gradient (Hoch and Korner, 2012). Considering the intimate linkages between the aboveground and belowground (Wardle et al., 2004), the change of resource quantity and quality input from plants to the belowground may affect the diversity and biomass pattern of litter invertebrates along elevational patterns. Forest ecosystems display more stable environmental conditions than meadows above the treeline, which have no protection from climate variations by woody canopies and shrub understories, (Heiniger et al., 2015). Harsh environments (e.g., low temperatures and more direct illumination at the ground level) in meadows may lower the energy-use efficiency (Wardle et al., 2004) of soil food webs. Plants at higher elevations, especially in a meadow above treeline, adapt to the harsh climate by increasing leaf toughness or by storing secondary metabolites (Cornelissen et al., 1999), which make more recalcitrant plant litter for invertebrates. Additionally, compared with meadows, the litter layer is thicker within forests and insulates the habitat of litter invertebrates from large swings in microclimatic conditions. Moreover, the continuing decrease in temperature in a meadow may have disproportionate effects on the higher trophic levels of food webs (Voigt et al., 2003). Therefore, the relative response of the different feeding guilds to environmental gradients may be ecosystem dependent, for example, higher omnivore abundance exists in woodlands whereas higher herbivore abundance exists in grasslands (Crotty et al., 2014). Many key ecosystem properties are altered at temperate treelines (Mayor et al., 2017), which may have profound effects on soil biota. However, we still have limited knowledge of how different feeding guilds of litter fauna related with each other below and above the treeline and the environmental correlates that underlie these patterns.

There are four major categories of environmental hypotheses that underlie the elevational diversity patterns of litter invertebrates: climatic, productivity, heterogeneity and soil property hypotheses (Werenkraut and Ruggiero, 2014). Variations in climate factors associated with elevation, such as temperature and precipitation, are important drivers for litter invertebrates (Palin et al., 2011). Food availability (resources production) has been suggested as a key factor that influences the relationships between richness/abundance and altitudinal