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Context dependency of the density–body mass relationship in litter invertebrates along an elevational gradient

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ABSTRACT

How community structure responds to environmental changes in space and time is a key concern in ecology. As a synthesized indicator of community structure, the density–body mass (DBM) relationship reflecting body size distributions can serve as a linkage between community response and ecological processes and function. However, the drivers of the spatial and temporal shifts in the DBM relationship for brown food webs remain largely unknown. This study aimed to find the elevational pattern of body size distributions of litter invertebrate communities and understand the causes of climate and resource factors shaping this pattern in different spatio-temporal contexts. We identified the elevational pattern of body size distributions of litter invertebrates in a temperate montane forest and, for the first time, examined this pattern by taking account of the temporal contexts integrating the growing and dormant seasons. Furthermore, we assessed the relative roles of climate factors (i.e., temperature, light, and moisture) and resource factors (i.e., litter quality and quantity) in body size distribution patterns. In general, we demonstrated litter invertebrate communities were size-structured at all elevations and in different seasons, which underpins the DBM. However, the elevational patterns of the DBM slopes varied between seasons: In the growing season the DBM slopes were shallower with increasing elevation. Contrasting, the DBM slopes were steeper with increasing elevation in the dormant season. This is indicating that along the elevation, the larger litter invertebrates benefited more in the growing season compared with the smaller invertebrates, which benefited more in the dormant season. The drivers of the DBM relationship were context dependent: (1) temperature was a fundamental driver for the DBM relationship across space and time, with increasing temperature benefiting smaller invertebrates; (2) crown density only matters in the dormant season, with increasing light intensity benefiting larger invertebrates. No impact of soil moisture on the body size distributions was detected; and (3) litter availability impact varied with season in quality (i.e., litter C:N and C:S ratios) and quantity (i.e., litter amount), mainly functioning in the growing and the dormant season, respectively. This finding would enhance a more predictive understanding of how environmental change may restructure ecosystems and soil functioning from an allometric scaling perspective in the context of global warming.

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1. Introduction

Community properties and their responses to environmental changes have long been a fundamental field of inquiry in ecology (Sundqvist et al., 2013). The questions as to whether and to what extent these responses can be predicted from the distribution of simple synoptic traits (e.g. body size) have recently been raised (Sutherland et al., 2013). Body size correlates with a host of ecological and demographic life-history traits, such as trophic status, diet width, secondary production, and nutrient cycling rate, which can affect the structure and dynamics of food webs across multiple scales of organization (Woodward et al., 2005; White et al., 2007). Density variance not only indicates population interactions with other species or the abiotic environment but also represents the success or failure of species' establishment in communities (Ott et al., 2014b). The allometric scaling between density (D) and body size (M) is thus important for understanding

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ecological processes (Damuth, 2007). The relationship between them has been well established as $D = aM^b$ in aquatic ecosystems and a world map of the marine diversity spectrum has been recently recorded (Webb, 2014). Pioneer studies (Mulder and Elser, 2009; Comor et al., 2014), which focus on topics ranging from body size distribution of soil biota to different environmental gradients, have made the density–body mass (DBM) relationship seem promising as a functional indicator (Turnbull et al., 2014) representing community structure and function responses to environmental change in terrestrial ecosystems.

Surprisingly, few studies have evaluated the DBM relationships in litter invertebrates, although they enhance the decomposition rates globally by 37% (Garcia-Palacios et al., 2013), which is significant for nutrient cycling, as most biomass (nearly 90%) (Cebrian, 1999) created by plants becomes "litter" after a plant dies. Body size distributions of litter-dwelling invertebrates can reflect the status of the community structure and the response to the decomposition dynamics and their interaction with spatio-temporal patterns of basal litter (Kominoski et al., 2011). Energy fluxes can also be derived from the allometric slope of the DBM regression. The slopes measure the relative occurrence of smaller species (microfauna) to large species (macrofauna) (Mulder, 2006), as the function of litter invertebrates in decomposition varies with body size. Large decomposers contribute by shredding the leaf litter into finer pieces and mixing fragments with the other layers of forest floor, while smaller invertebrates contribute to the decomposition by indirectly interacting with microflora as well as directly consuming leaf nutrients (Wardle et al., 2004). The DBM slope can thus be regarded as a useful currency that indicates resource allocation among species (White et al., 2007) and reflects biotic and abiotic environmental conditions related to both biological and ecological functioning (Mulder et al., 2011).

Climate change may become major drivers affecting the structure and functioning of ecological assemblages over the next several decades (Brose et al., 2012). Increasing temperatures can affect DBM relationship by accelerating individuals' metabolism rates in cellular levels thus altering population biomass density distributions, particularly for invertebrates (Gillooly et al., 2001; Brown et al., 2004). A global study on aquatic ecosystems shows that increasing temperature benefits smaller animals more than large ones (Daufresne et al., 2009). Changes of other ecologically significant climate factors, such as precipitation (Lindo et al., 2012; Sylvain et al., 2014) and irradiance (Richardson et al., 2010), are also likely to have profound effects on the size structure of litter communities. In addition to climate factors, resource availability including the quality (Ott et al., 2014b) and production (Comor et al., 2014) of basal food resources, is probably another important factor contributing to the dynamics of DBM relationships. Previous studies mainly considered climate factors and resource availability separately; in reality, however, these factors often may act simultaneously and may function in combination.

The drivers of body size distribution in litter invertebrates may be of time-dependent. All individuals in natural communities have passed through intra- and inter- annual ongoing variance. Apart from phenology, driven by climatic factors in different seasons (Montoya and Raffaelli, 2010), litter invertebrate communities are affected by the temporal dynamics of basal resources (Berg and Bengtsson, 2007; Hastings, 2012). Compared to dwelling on the rapid decomposing litter in growing seasons, invertebrates in deciduous forest floors mainly live in the fresh organic matter (FOM) due to pulse-like leaf litter input to the belowground system (Yang et al., 2008) in dormant seasons. The patterns and drivers of the DBM relationship may differ as resource status and climate conditions vary with seasons. Although size-driven community variations in soil invertebrates are increasingly being documented (Mulder and Elser, 2009; Comor et al., 2014; Ott et al., 2014a, 2014b), the patterns and drivers of temporal shifts in body size distribution for the dynamics of brown food webs remain largely unknown.

Elevational gradients can provide ideal natural experiments (Sundqvist et al., 2013) for evaluating the combined effects of temperature and other environmental variables on the DBM relationship for a number of reasons. First, studies on elevational gradients can be repeated at multiple locations around the world, making it possible to test for the generality of the underlying causes (McCain, 2009). Second, temperature and other environmental variables (e.g., precipitation, light condition, and resource property) often covary with elevation, although not in a similar manner across different elevational gradients (Korner, 2007). Third, field data can be collected more readily along elevational gradients, as the spatial extent of elevational gradients is small in comparison with latitudinal gradients (Sanders and Rahbek, 2012). Furthermore, elevational gradients can contribute to our understanding of ecosystem responses to global climate change at much larger spatial and temporal scales than is possible through conventional ecological experiments (Sundqvist et al., 2013).

In this study, we identified the patterns and drivers of the DBM relationship in litter invertebrates along an elevational gradient across the growing and dormant seasons. We assumed that temperature and other abiotic variables change with elevation, and the context change alters the quantity and quality of litter resource for invertebrates dwelling in. Therefore, the combination of the changes will readily affect the size structure of litter dwelling communities (Fig. 1). We aimed to answer three questions: (1) in general, whether the DBM relationship exists in litter invertebrates at all elevations across space and time? (2) if it exists, how does the DBM relationship change with the elevation in different seasons, and do larger invertebrates benefit more along the elevational gradient? and (3) if the previous two questions can be answered affirmatively, then what are the drivers of the dynamics of the DBM relationship in litter communities and their relative roles in determining this relationship?

2. Material and methods

2.1. Study sites and sampling period

The study area was selected at the Beijing Forest Ecosystem Research Station of the Chinese Academy of Sciences, which is located

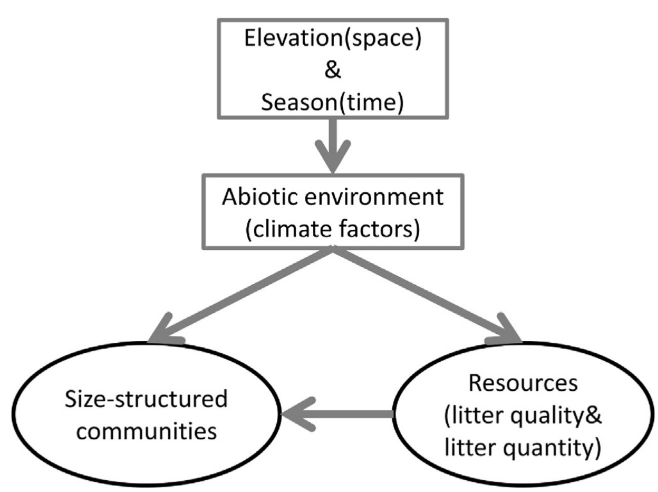

Fig. 1. Hypothesis framework. We hypothesized that abiotic variables (particularly climate factors) which often covaried with the elevation altered resource quantity and quality for litter invertebrates and the combination of them would ultimately affect size-structured litter-dwelling communities.

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