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

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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.

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...
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% (García-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 a major driver affecting the structure and functioning of ecological assemblages over the next several decades (Brose et al., 2012). Increasing temperature can affect DBM relationships 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 (Lindetaal, 2012; Sylvaineaal, 2014) and irradiance (Richardsoneal, 2010), are also likely to have profound effects on the size structure of litter communities. In addition to climate factors, resource availability including the inequality (Ott et al., 2014b) and productivity (Comoretal, 2014) of basal food resources is probably the most 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 relationships 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 (Körner, 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 (Sanderson 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 climatic 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...
on Dongling Mountain (40°00′−40°02′N, 115°26′−115°30′E), 100 km northwest of Beijing City, China. The soil type in this area was brown soil that was comprised mainly of Eutric cambisol (FAO, 1988). This area had a typical warm temperate continental monsoon climate with an average annual precipitation of 500−650 mm (the precipitation in winter is snow), which occurred mainly in June through August (approximately 78% of the total precipitation). The mean annual temperature was 5−10°C, ranging from 18.3°C in the hottest month (July) to 10.1°C in the coldest (January). The annual frost-free period was approximately 195 d, with approximately 2600 h of sunshine. The zonal vegetation of the study area was highly heterogeneous warm temperate zone deciduous broad-leaved forest, including mainly 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 included some conifers and certain shrubs (e.g., Prunus spp., Vixx negundo var. heterophylla, etc.).

Field work was conducted in six transects dominated by oak (Quercus wutaishanica) that were selected mainly based on the elevation range from 1000 m to 1800 m. The six transects each occupy a different elevational segment, and together form a single elevational gradient. The transects varied little in terms of the terrain slope (approximately 30°) and orientation (the west-facing sunny slope). In the middle of each transect, a 10 m × 10 m plot was chosen. The elevation (length of the transect) of chosen plots were: 1040 asl (80 m), 1104 asl (180 m), 1284 asl (130 m), 1444 asl (140 m), 1640 asl (110 m), and 1725 asl (170 m), respectively. On six elevations, we sampled 3 parallel line transects, 4 m apart from each other. Along each line transect we sampled 3 subplots (0.5 × 0.5 m), again spaced in 4 m distance. Subsamples from each line transect were pooled, leading to 3 replicates per elevation and in total to 18 replicates per season across all elevations. In addition to an aboveground plant diversity investigation conducted in August, we performed the same investigation in the same plot in late October in 2012, respectively representing the growing season and the dormant season.

2.2. Soil fauna collection, identification, and construction of the DBM relationships

On each subplot, we applied two methods to categorize the animals into different size classes: (1) hand-sorting animals in the subplots to obtain the large animals; and (2) collecting leaf litter from the OL horizon and the humus layer (the OF and OH horizons) in a cotton bag and taking it back to extract meso- and microfauna. The extraction was done in double-cone Tullgren funnels with a an outer diameter of 5 cm and three samples per plot). Soil pH had been measured using Mettler Toledo FE20k using 10 g of soil and 25 ml of CaCl₂ solution. Litter richness was represented by the tree and shrub richness in the growing season and by plant richness in August, including trees, shrubs, and the herb layer in the dormant season. Litter amount was represented by litter thickness (Aznar et al., 2010) above the humus layer (OF and OH horizons). Leaf litter was also collected and dried at 60°C until there was no further weight loss. After being thoroughly mixed, the leaf litter from each subplot was grounded to powder with a ball mill. The powder from three subplots per plot was merged into a mixed sample to ensure the homogeneity and representativeness of the samples. We got a total of 18 samples at each season with three replications in each elevation. We analyzed the element contents (carbon, nitrogen, and sulfur) of the litter by using an automated CHNSO analyzer (Elementar Vario El. III, Elementar Analysensysteme GmbH, Hanau, GE). Finally, the litter quality was represented by litter C:N and C:S ratios, considering that carbon, nitrogen, and sulfur are the three nutrients that are cycled between the soil, plant matter, and the atmosphere.

2.4. Statistical analyses

First, we determined the relationship of environmental variables and litter properties to elevation using the Pearson correlation index and Ordinary Least Square (OLS) regression. OLS regression was also applied to construct the DBM relationship and determine the pattern of DBM slopes along the elevational gradient. Then, to determine the most significant factors influencing the slopes of DBM and their relative weights, stepwise regression (backwards method to eliminate multicollinearity among different observation variables) based on Akaike’s information criterion (AIC) was used to select the best-fitting model with the lowest AIC, based on which Anova comparison was used to obtain a simpler final model containing less terms. We used the global validation linear model assumptions to diagnose whether...
our data meet the criteria or the assumptions applying linear model.

To discuss the possible paths between the drivers of DBM relationship, we employed the Maximum Likelihood (ML) method to generate a structural equation model based on the results of the stepwise regression and the known effects. Aside from the slopes of the DBM (all negative), all the variables were log transformed before the structural equation analysis was conducted.

Correlation analyses, OLS regressions, stepwise regressions, and model diagnoses were all conducted in R 3.0.3 using “PerformanceAnalytics,” “MASS,” “car,” and “gvlma” packages, respectively. The standardized effects of variables on the structural equation model were analyzed using SAS 9.3.

3. Results

3.1. Environmental variables and resource property response to elevation

In the growing season (Table 1 and Table S1 in Appendix S2), temperature (r = −0.92, p < 0.001) and litter richness (r = −0.71, p < 0.001) were negatively correlated with elevation. While water content (r = 0.58, p < 0.05), litter thickness (r = 0.50, p < 0.05), and litter C:S ratio (r = 0.91, p < 0.001) were positively correlated with elevation. However, in the dormant season (Table 1), litter thickness (r = 0.65, p < 0.01) and litter C:S ratio (r = 0.62, p < 0.01) were positively correlated with elevation. Surprisingly, temperature (r = 0.95, p < 0.001) also demonstrated a positive correlation.

3.2. DBM relationships of litter invertebrates’ response to elevation

There are 87 families (or morphospecies) across 28 orders sampled in the 12 plots, yielding a total of 319 categories and 11,354 individuals. Collembola, Acariformes, and Diptera (37.88%, 27.56%, 14.81%, respectively, of the total individuals) were the dominant orders in the dormant season. Fewer individuals (1682 versus 9672) and orders (13 versus 25) of animals were found in the dormant seasons (See Appendix S3).

DBM relationships of the litter invertebrates were generated (p < 0.05) in both the growing and the dormant seasons at all elevations (Figs. 2 and 3). The slope of DBM in the growing season (−0.3959) was lower than that in the dormant season (−0.2839), while far more taxa (10 versus 3 classes) were activated in the growing season. Contrasting patterns of the DBM slopes with elevation were observed in different seasons, increasing with elevation in the growing season and decreasing with elevation in the dormant season (Fig. 4).

3.3. Environmental variables and resource property association with the DBM relationship

We obtained the best-fitting model based on stepwise regressions (Table 2, Table S2 in Appendix S2) and the final model was constructed using Anova comparison (Table S3 in Appendix S2). The variance inflation factor for the final model (Table S4 in Appendix S2) showed that the multicollinearity between environmental factors was almost eliminated (VIF values were less than 4) after stepwise regressions. In general, the final model accounted for 93.8% and 93.38% variance of the DBM slopes, respectively, in the growing season and the dormant season.

We calculated the relative weight of each factor entered into the best-fitting model on the variance of the slope of the DBM relationship based on stepwise regressions (Table 2, Tables S2 and S3 in Appendix S2). Temperature occupied the highest relative weight to the slope of the DBM in both seasons, explaining 50.44% (relative weight) of the total variance (93.8%) in growing season and 66.38% (relative weight) in dormant season (93.38%). Litter C:N (29.93% of total variance, p = 0.003) and C:S (19.63% of total variance, p < 0.001) ratios also had a significant influence on the DBM relationship in the growing season (Fig. 5a). In the dormant season (Fig. 5b), litter richness explained 21.92% (p < 0.001) of the DBM relationship, while litter thickness (8.10%, p = 0.0183) and crown density (3.60%, p = 0.0125) also had an impact.

4. Discussion

Context dependence of size structured litter invertebrate communities is crucial to fully understand the interaction between the litter and the invertebrates. The response of the invertebrates to the litter they living in is affected by climate and resource availability varied in space and time. The separate effects of these factors have been studied in recent years (Mulder and Eiser, 2009; Brose et al., 2012). However, the combined effects of these factors on the interaction are far from clear. Conceiving that former studies mainly focused on a specific aspect of the issue, a synthesized study

Table 1

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<th>Response of environmental variables and resource properties to the elevation.</th>
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<td><strong>Estimate</strong></td>
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<td>Temperature</td>
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<td>Crown density</td>
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<td><strong>Dormant season</strong></td>
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Values in bold indicate significant correlations (P < 0.05).
the growing season and seasons. Unexpectedly, temperature was found to increase with changes along with the elevation across the growing and dormant study, we identified temperature as the strongest and most consistent driver of the DBM relationship along the elevational gradient (Fig. 5). The steeper (more negative) slope of the DBM as the temperature increases infers that warming benefits smaller more than larger invertebrates. The same conclusion could be inferred from the shallower DBM slopes in the dormant season than those in the growing season, no matter as a whole (Fig. 2) or on each elevation (Fig. 3). We can infer that it is a constant result that smaller invertebrates are benefiting more from the increasing temperature in both small (about 3.5 °C) and large ranges (about 20 °C) of temperature changes. This result is in line with a study on aquatic ecosystems (Daufresne et al., 2009) and provides additional evidence that Bergmann’s rule, which initially explained the positive relationship between body size and latitude in endotherms (Gardner et al., 2011) can also be applied to ectotherms. According to the metabolic theory of ecology (MTE), temperature and body size are two significant factors that affect the most fundamental biological rates, the metabolic rates at which organisms take up, transform and expend energy and materials (Brown et al., 2004). The temperature-induced shifts of body size distribution in litter invertebrates combined with the changes in the temperature per se, may alter the metabolic rates of entire communities, which would ultimately affect the function of litter-dwelling invertebrates in decomposition processes and nutrient cycling. A number of studies demonstrate that temperature is critical to litter qualities and quantities in the decomposition dynamics (Fierer et al., 2005; Davidson and Janssens, 2006). We found that the litter C:S ratio negatively correlated with temperature in the growing season and litter thickness positively correlated with temperature in the dormant season (Table 1) in the dormant season, which is the exact opposite of the traditional understanding. We examined three years of temperature records for the same period of time and found similar patterns along the elevational gradient (unpublished data). This finding was probably the result of employing the soil temperature, which may not always demonstrate the same declining trends as air temperature, dropping 5.5 K per kilometer of altitude on average. Under the cover of vegetation, particularly in a montane forest with complex architecture (Poorter et al., 2006) and topography, soil temperature could effectively decouple from free convection by generating an aerodynamic resistance against heat exchange (Körner, 2007) and could warm significantly under solar radiation (Fernandez and FETCHER, 1991). We found that crown density was negatively correlated with the DBM relationships in the dormant season, leading to a steeper slope (more negative) representing large animals benefited from the increasing light intensity which is negatively correlated with the crown density (King et al., 2005). Higher light intensity in winter usually means more energy input. Light may enhance microbial activity by increasing the nutrient uptake (such as phosphorus) (Duhamel et al., 2012) and thus facilitate invertebrate growth.

Our results identified temperature as the strongest and most consistent driver of the DBM relationship along the elevational gradient (Fig. 5). The steeper (more negative) slope of the DBM as the temperature increases infers that warming benefits smaller more than larger invertebrates. The same conclusion could be inferred from the shallower DBM slopes in the dormant season than those in the growing season, no matter as a whole (Fig. 2) or on each elevation (Fig. 3). We can infer that it is a constant result that smaller invertebrates are benefiting more from the increasing temperature in both small (about 3.5 °C) and large ranges (about 20 °C) of temperature changes. This result is in line with a study on aquatic ecosystems (Daufresne et al., 2009) and provides additional evidence that Bergmann’s rule, which initially explained the positive relationship between body size and latitude in endotherms (Gardner et al., 2011) can also be applied to ectotherms. According to the metabolic theory of ecology (MTE), temperature and body size are two significant factors that affect the most fundamental biological rates, the metabolic rates at which organisms take up, transform and expend energy and materials (Brown et al., 2004). The temperature-induced shifts of body size distribution in litter invertebrates combined with the changes in the temperature per se, may alter the metabolic rates of entire communities, which would ultimately affect the function of litter-dwelling invertebrates in decomposition processes and nutrient cycling. A number of studies demonstrate that temperature is critical to litter qualities and quantities in the decomposition dynamics (Fierer et al., 2005; Davidson and Janssens, 2006). We found that the litter C:S ratio negatively correlated with temperature in the growing season and litter thickness positively correlated with temperature in the dormant season (Table S1 in Appendix S2). These correlations were also supported by structural equation model (SEM) analysis (Fig. 6). We applied the SEM analysis to make our hypothesis framework more visual to show the possible paths between the different variables, although using the small samples to conduct SEM and ML extrapolation might lead to biased results. Temperature might affect litter C:S ratios negatively and litter C:N ratios positively in the growing season, while affecting litter thickness positively in the dormant season. Thus, in addition to having a direct impact on animal size, temperature can also affect the DBM relationship by altering the availability of basal resources for invertebrates.

Fig. 2. DBM relationships of all elevations in different seasons. Letter “a” represents the growing season and “b” represents the dormant season.

4.1. Temperature

According to the IPCC report, average global surface temperatures will rise by at least 2 °C by the year 2100, with stronger increases experiencing in land surfaces and mountain ranges (IPCC, 2007). A pressing issue is predicting how climate and other relevant environmental factors affect ecosystem processes and functioning. In this study, we identified litter invertebrates’ response to temperature changes along with the elevation across the growing and dormant seasons. Unexpectedly, temperature was found to increase with
Fig. 3. DBM relationships of each elevation in different seasons. Letters “a” to “f” represent plots with different elevations in the growing seasons, and “g” to “l” represent plots with different elevations in dormant seasons.
substances in ecological interactions and processes (Sterner and Elser, 2002). Constructed of multiple elements, organisms often require different elemental ratios provided by their resources (Moe et al., 2005). The mismatch between demand and supply operates at all levels of ecological interfaces and serves as the core of ecological stoichiometry (Sterner and Elser, 2002). We utilized litter stoichiometry (litter C:N and C:S ratios) to represent resource quality and found contrasting relations between the DBM slopes and litter C:N and C:S ratios in the growing season. The negative correlation (Table 2) between the slope of DBM and litter C:N ratio (a higher C:N generates a steeper (more negative) slope) illustrated that larger organisms benefited more from greater amount of nitrogen (N). In contrast, the DBM slope positively correlated with litter C:S ratio (Table 2), indicating smaller invertebrates benefited more from relatively higher amount of sulfur (S). The correlation between the C:N ratio and DBM slope is in line with some large-scale studies of soil invertebrates in grassland (Mulder and Elser, 2009). We can infer that nitrogen is critical for the growth of soil invertebrates in terms of its general importance for the production of nucleic acids and structural components (proteins, silk, and chitin) (Kaspari and Yanoviak, 2009). In light of the fact that most invertebrates rely heavily on microorganisms and fungi (Scheu, 2002), as they lack the necessary enzymes to digest litter material directly, a possible reason for the constrained effect of sulfur on invertebrate growth is that a higher sulfur diet may limit microbial activity (Dursun et al., 1996), thus hindering the resource take-up rates and ultimately impeding the growth of litter animals.

Table 2
Environmental factors affect the slope of DBM in the best model.

|                              | Estimate | t value | AIC   | Delta AIC | Pr(|t|) |
|------------------------------|----------|---------|-------|-----------|--------|
| **Growing season**           |          |         |       |           |        |
| Full model                   |          |         |       |           |        |
| Litter thickness             | 0.0051   | 2.115   | −164.96 | 0         | <0.001 |
| Litter C:N ratio             | −0.0045  | −3.63   | −161.64 | 3.32      | 0.0543 |
| Temperature                  | −0.0159  | −4.201  | −154.36 | 10.6      | 0.0031 |
| Litter C:S ratio             | 0.0002   | 4.456   | −150.27 | 14.69     | <0.001 |
| **Dormant season**           |          |         |       |           |        |
| Full model                   |          |         |       |           |        |
| Litter C:N ratio             | −0.0007  | −1.408  | −161.99 | 0.76      | 0.1844 |
| Litter thickness             | 0.0089   | 2.729   | −156.06 | 6.69      | 0.0183 |
| Crown density                | −0.0926  | −2.934  | −155.01 | 7.74      | 0.0125 |
| Litter richness              | −0.0029  | −0.542  | −137.41 | 25.34     | <0.001 |
| Temperature                  | −0.0415  | −9.651  | −125.68 | 37.04     | <0.001 |

Values in bold indicate significant correlations (P < 0.05).

Fig. 4. Contrasting patterns of the DBM relationship in different seasons. Letter “a” represents the growing season and “b” represents the dormant season.

Fig. 5. Relative weight of environmental variables at different seasons. Letter “a” represents the growing season and “b” represents the dormant season. The R square showed in the middle part of the panel was the total variation accounting for the DBM slopes in the final model.
demonstrating that higher productivity benefits smaller soil animals (Chen and Wise, 1999; Tiefs et al., 2008; Comor et al., 2014). This discrepancy may be because mites, insect larvae, and collembolans, in particular, constitute the main decomposer communities dwelling on fresh organic matter (FOM) in dormant seasons. As the essential decomposers in surface litter, collembolans prefer FOM (Loreau et al., 2002) and fungal hyphae (Fontaine and Barot, 2005) as their main food. Thus, the fungal-based energy channel with a highly efficient transfer of energy to higher trophic levels (insect larvae and some predator mites) becomes dominant (Wardle et al., 2004) in dormant seasons, ultimately benefiting large animals more.

4.4. Caveats

We constructed the density–body mass relationship of litter invertebrates using LSDR models based on family or morphospecies levels constrained by the classification knowledge of litter invertebrates. Family or morphospecies is a medium resolution between orders (low resolution) and species (high resolution). Previous studies have sorted and sized soil fauna at the genus level to facilitate analysis. However, lower resolution may generate “noise” as well as sacrifice functionality. Although the density–body mass relationship was constructed based on family or morphospecies level, we still detected the DBM slope response to environmental change. Our work supports the posit morphotyping to a genus equivalent level to construct the DBM relationship is reasonable (Turnbull et al., 2014).

Considering the natural complexity of ecological communities, ecologists often collect elaborate data sets including confounding factors. Multicollinearity of confounded explanatory variables may threaten statistical and inferential interpretation of the multiple regression (Graham, 2003). Although we used the stepwise regression to eliminate the multicollinearity, some variables contained in the final models still correlated (e.g., the negative correlation between litter C:S ratio and temperature in the growing season, and the positive correlation between litter thickness and temperature). The variance inflation (VIF) values that exceed 10 are often regarded as indicating multicollinearity (Belsley et al., 2005). All the variance inflation values in the final model are less than 4, so we can infer that the final multiple regression models are still valid and credible. Future studies integrating natural gradient (e.g., elevational gradient) with experimental manipulations may help disentangle the separate and combined effects of climate factors and resource availability on community structure.

5. Conclusion

Shifts of body size distributions reflecting energetic allocation dynamics of different body mass categories may have knock-on consequences for community stability and ecosystem functioning. We found a contrasting pattern of DBM relationships in litter invertebrate communities along an elevational gradient across the two seasons, indicating that larger invertebrates benefit more in the growing season compared with the smaller ones, which benefit more in the dormant season. The drivers of the DBM relationship were context dependent in that temperature was a fundamental driver for the dynamics of body size distributions across seasons while the litter impact varied with the seasons in quality and quantity. Integration of temperature and basal resource availability effects with the spatio-temporal dynamics of body size distributions disclosed the responding process and mechanism of invertebrates to litter pulse-like changes in a temperate forest, which can enhance a more predictive understanding on how climate change may restructure ecosystems.

Fig. 6. Structure equation model in different seasons. Letter “a” represents the growing season and “b” represents the dormant season. The width of the arrows indicates the strength of the standardized path coefficient. The solid lines indicate positive path coefficients and dashed lines indicate negative path coefficients, values represent the proportion of the variance explained for each endogenous variable. Signif. codes: “****” represents <0.001, “***” <0.01, “**” <0.05.
Statement of authorship

GRX, SZ, KMM, and YHL designed the experiment. GRX and SZ did the field investigation. GRX identified the invertebrates and measure the litter elemental contents in lab. Statistical procedures were performed by GRX and SZ. GRX wrote the first draft of the manuscript, and all authors contributed substantially to the manuscript.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.soilbio.2015.06.010.

References


