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

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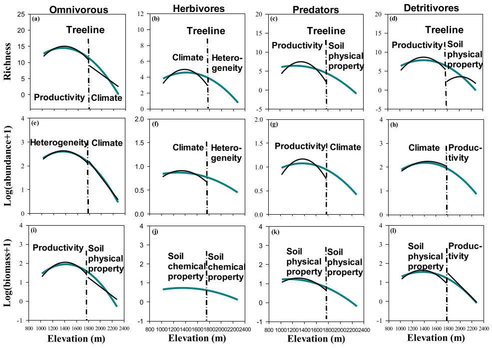
HIGHLIGHTS

- 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



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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

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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 gradients (Blackburn and Gaston, 2001). Litter mass and litter thickness have also been found to be important for the richness or biomass of litter invertebrates in several feeding guilds (Jochum et al., 2017; Ott et al., 2014). Climate-change-induced shifts in plant characteristics and vegetation type have also been suggested as determinants in the structuring of communities of soil biota (Ettema and Wardle, 2002; Minor et al., 2016) by influencing the quality and quantity of available resources present in the soil (Wardle et al., 2004). Plant richness affects the abundance and richness of higher trophic levels (Haddad et al., 2009; Scherber et al., 2010) and woody plant richness has also been reported to have few effects on invertebrates (Schuldt et al., 2014). The physical structure and heterogeneity of the soil habitat represented by the particle size distribution regulates engineering activities, such as burrowing, casting, and nesting activities, and may affect the distribution of litter invertebrates (Nielsen et al., 2008). Moreover, soil chemical factors, such as pH and the availability of nutrients (e.g., C, N, and P), are also strongly related to soil biota (Loranger et al., 2001; Mulder and Elser, 2009). To date, few studies have evaluated if the environmental correlates that drive the elevational diversity patterns of different feeding guilds of litter invertebrates shift at treelines.

In this paper, we used an oak-dominated forest transect (from 1020 to 1770 asl) that shifts to a meadow gradient (from 1790 to 2280 asl) up to a mountain top as a model system for investigating changes in feeding guilds of litter invertebrate communities. Based on this study system, we had previously compared the elevational patterns of all soil-dwelling and litter-dwelling invertebrates and found that litter invertebrates were more sensitive to elevational change both in forests and meadows (Xu et al., 2017). The elevational patterns of litter invertebrates shifted from hump-shaped elevational patterns to declining patterns at the treeline. The dominant environment predictors of the richness and abundance patterns of litter-dwelling invertebrates were productivity in the forest below the treeline and climate in the meadow above the treeline (Xu et al., 2017). The main goal of the present study is to apply the same statistical techniques 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 a treeline. We assessed richness, abundance, and biomass patterns of litter invertebrates across four different feeding guilds (omnivores, herbivores, detritivores, and predators) along an elevation gradient under below-treeline forest and above-treeline meadow, respectively. In particular, we (i) explored the elevational patterns of richness, abundance, and biomass across the treeline, (ii) tested if these elevational patterns of different feeding guilds were correlated with one another in the forest or meadow, and (iii) compared the environmental predictors for these patterns below and above the treeline.

2. Materials and methods

2.1. Study area

We chose the Beijing Forest Ecosystem Research Station of the Chinese Academy of Sciences (40°00″–40°03″N and 115°26″–115°30″E) as the study area, situated on Dongling Mountain, approximately 100 km northwest of Beijing city, China. This area has a typical warm temperate continental monsoon climate. The average annual precipitation is 500–650 mm and mean annual temperature is 5–10 °C. Brown soil is the main soil type and is mainly comprised of Eutric cambisol (FAO, 1988). The zonal vegetation in forests 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 dominant species in subalpine meadow mainly include *Saussurea purpurascens*, *Carex capillaris*, and *Iris ruthenicar*.

We chose a forest elevational gradient dominated by *Q. liaotungensis* that ranged from 1020 m asl (near the base of Dongling Mountain) to 1770 m asl and a meadow elevational gradient that ranged from 1790 m asl to 2280 m asl (close to the summit of the Dongling Mountain). The 10 transects, each occupying a different elevational segment of the slopes, together formed a single montane forest elevational gradient. The lengths of the 10-m-wide transects ranged from 80 m to 180 m. Each transect was divided into 10 m × 10 m plots (parallel to the slope), with a total of 119 plots (one plot at one elevation) in the forest (see Fig. S1, the sketch map on sampling transects, in Appendix A). Above the treeline, 21 plots (10 m × 10 m) at approximately 20-m-elevational intervals along the mountain were also chosen to form an elevational gradient of subalpine meadow. A total of 140 plots were selected for this study and were surveyed along the elevational gradient across the forest and subalpine meadow. Each plot was chosen with approximately the same aspect (western slope) and similar slopes (between 22° and 48°) to ensure that climate served as the major abiotic driver that varied with elevation in this system. The elevation, latitude, and longitude of each plot were logged by a GPS unit. More details on the study area and plant community investigation can be found in a previous study (Xu et al., 2017).

2.2. Litter animal collection and identification

Three mechanically selected (along the diagonal line of each plot) subplots (1 m × 1 m) were set in each 10 m × 10 m plot. We applied two methods to sample litter invertebrates in each subplot: (1) animals in the three 0.6 m × 0.6 m subplots were hand-sorted to obtain the large animals that could be seen by the naked eye and (2) all leaf litter from the OL horizon and the humus layer (the OF and OH horizons) in the subplot were collected, placed into a cotton bag and retrieved to extract meso- and micro-fauna. Each sample was placed in a cotton bag to ensure that the activity of animals was unaffected and was then 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. Most litter invertebrates were identified to the family or morphospecies level, except for Mesostigmata and Prostigmata, which were identified at a suborder level. Because of the great differences in their morphologies, food resources, and ecological roles in food webs, the adults and larvae of beetles were analyzed as different morphospecies. We recorded the taxonomic identities, the abundance of invertebrates and the body length (for 10 individuals for each taxon or all individuals when <10) for each plot. 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 evaluated the biomass of each family or morphospecies. We divided litter invertebrates into four functional guilds based on feeding regime: omnivores (feed on several trophic levels), herbivores, predators, and detritivores (feed on dead animal and plant material); the division was based on previous studies (Illig et al., 2005; Moreira et al., 2008; Moretti et al., 2016) as well as a combined knowledge of the resources they usually use and their mouthparts (see details in Appendix B).

2.3. Environmental variables assessment

Environmental variables were divided into four different groups based on the different hypotheses underlying the biodiversity elevational patterns: (1) Climate included mean annual temperature (MAT), mean annual temperature range (TVAR), sampling temperature (TINS), and mean annual precipitation (MAP). (2) Productivity included woody cover (WOODYCOV), herb cover (HERBCOV), basal area (BASEA), and litter thickness (LITTERTH). (3) Resource heterogeneity included woody plant species richness (TSRICH) and herbaceous plant species richness (HERBRICH). (4) Soil characteristics were further divided into soil physical and chemical characteristics. Soil physical characteristics included soil moisture, bulk density (BULKDEN), soil conductivity, and soil texture (percentage of clay, silt, and sand); soil chemical characteristics included soil pH, total nitrogen (TN) and phosphorus (TP) content, available nitrogen (AN) and phosphorus (AP) content, C:N ratios and C:P ratios (calculated based on the total carbon, nitrogen, and phosphorus content). Details for measuring the environmental variables mentioned above can be seen in Appendix C and followed standard procedures.

2.4. Statistical analyses

2.4.1. Estimation of elevational patterns of different feeding guilds in litter invertebrates

Ordinary least squares regression with a first- or second-order polynomial was used to determine the elevation patterns in richness, abundance, and biomass of different feeding guilds in litter invertebrates. Abundance and biomass data were $\log(x + 1)$ transformed prior to analysis to improve normality.

The relationships between richness and abundance or biomass of different feeding guilds were separately estimated in forest and meadow by Pearson correlation.

2.4.2. Association assessment of richness, abundance, and biomass of litter invertebrates with environmental variables

We tested the environmental hypotheses by following three steps using SAM 4.0 (Burnham and Anderson, 2002; Werenkraut and Ruggiero, 2014). First, we independently assessed each hypothesis in an exhaustive search. The model with the lowest corrected Akaike's information criterion value (AICc) was selected as the best single statistical model. Then, we selected the best predictors in each single hypothesis by conducting model averaging and calculating the relative importance (w_i) of each environmental variable. Finally, the best composite model was generated by including all important environmental variables in the best single statistical model and variables with $w_i >$ 0.9 in the other models (Burnham and Anderson, 2002). Forest and meadow elevational gradients were separately evaluated. Spatial autoregression was considered by incorporating eigenvector-based spatial filters calculated from the geographic distances in all the models (Rangel et al., 2010). Appendix D provides the multi-model inferring details for the final models.

We quantified the relative contribution of environmental variables included in the final model and elevation to the variances of richness, abundance, and biomass in the following four categories: (1) the effect of environmental predictors alone, (2) the shared effect of environmental predictors and elevation, (3) the effect of elevation alone, and (4) unexplained variance (Werenkraut and Ruggiero, 2014).

3. Results

3.1. Composition summary of litter invertebrates in different feeding guilds

In the forest, the abundance and biomass of different feeding guilds in decreasing order were omnivores, detritivores, predators, and herbivores (Table 1). The richness of herbivores and predators were more than that of omnivores in the forest, whereas herbivore richness was more than that of the other three functional groups in the meadow. In total, the richness, abundance, and biomass in all feeding guilds in the forest were all more than those in the meadow.

3.2. Elevational richness, abundance and biomass patterns of litter invertebrates in different feeding guilds

Richness, abundance and biomass of the litter invertebrates in all feeding guilds showed hump-shaped patterns along the entire elevational gradient (Fig. 1). The hump-shaped patterns were mainly driven by the variances in the forest, except for the biomass of herbivores, which showed no pattern (Fig. 1j). In the meadow, the richness, abundance, and biomass of omnivores declined with increasing elevation (Fig. 1a,e,i), whereas there were no patterns in those properties for herbivores (Fig. 1b,f,j) and predators (Fig. 1c,g,k). Interestingly, detritivores showed a repeated hump-shaped pattern in richness (Fig. 1d), no pattern in abundance (Fig. 1h) and a monotonically decreasing pattern in biomass along the elevational gradient in the meadow.

In the forest, the richness and abundance of different feeding guilds were significantly positively correlated (Table 2, lower triangular matrix). The biomass of omnivores was also positively related to that of predators and detritivores, whereas in the meadow (Table 2, upper triangular matrix), the richness, abundance, and biomass of different feeding guilds were not correlated, except that the richness of omnivores was significantly positively correlated with that of predators.

3.3. Underlying environmental correlates with elevational richness, abundance, and biomass patterns of litter invertebrates in different feeding guilds

In the forest, the variances of richness in omnivores, predators, and detritivores were best explained by litter thickness, which supports the productivity hypothesis (Table 3). For herbivores, the variances of both richness and abundance were best correlated with mean annual precipitation, which supports the climate hypothesis. The abundance of omnivores was negatively correlated with woody and herbaceous plant richness (heterogeneity), whereas that of predators was positively correlated with litter thickness (productivity) and that of detritivores was positively correlated with mean annual precipitation and mean annual temperature range (Climate). The variance of biomass in omnivores was best explained by litter thickness and basal area, which supports the productivity hypothesis. For predators and detritivores, biomass was significantly positively related to soil bulk density and soil moisture content (soil physical property).

Environmental correlates that accounted for richness, abundance, and biomass of feeding guilds changed in the meadow. Above the treeline, the variances of richness and abundance in omnivores were most explained by the mean annual temperature, supporting the climate hypothesis (Table 3), whereas the variance of biomass was negatively correlated with soil conductivity (soil physical property). For herbivores, the richness and abundance variances were best positively related to herbaceous plant richness, which supports the heterogeneity hypothesis. The biomass of herbivores was negatively correlated with soil N content but positively correlated with total P content and C:P

Table 1
Composition summary of litter invertebrates in different feeding guilds along the elevational gradient in Dongling Mountain.

Vegetation	Response variable	Families/morphospecies	Orders	Classes	Individuals	Biomass(mg)
Forest	Omnivores	28	14	7	41,875	9,896.18
	Herbivores	33	11	2	812	1,148.43
	Predators	33	9	3	1,388	5,904.78
	Detritivores	27	11	5	17,944	8,710.23
Meadow	Omnivores	14	7	4	1,923	204.32
	Herbivores	18	7	1	80	31.61
	Predators	14	6	3	106	34.64
	Detritivores	13	7	5	565	552.52

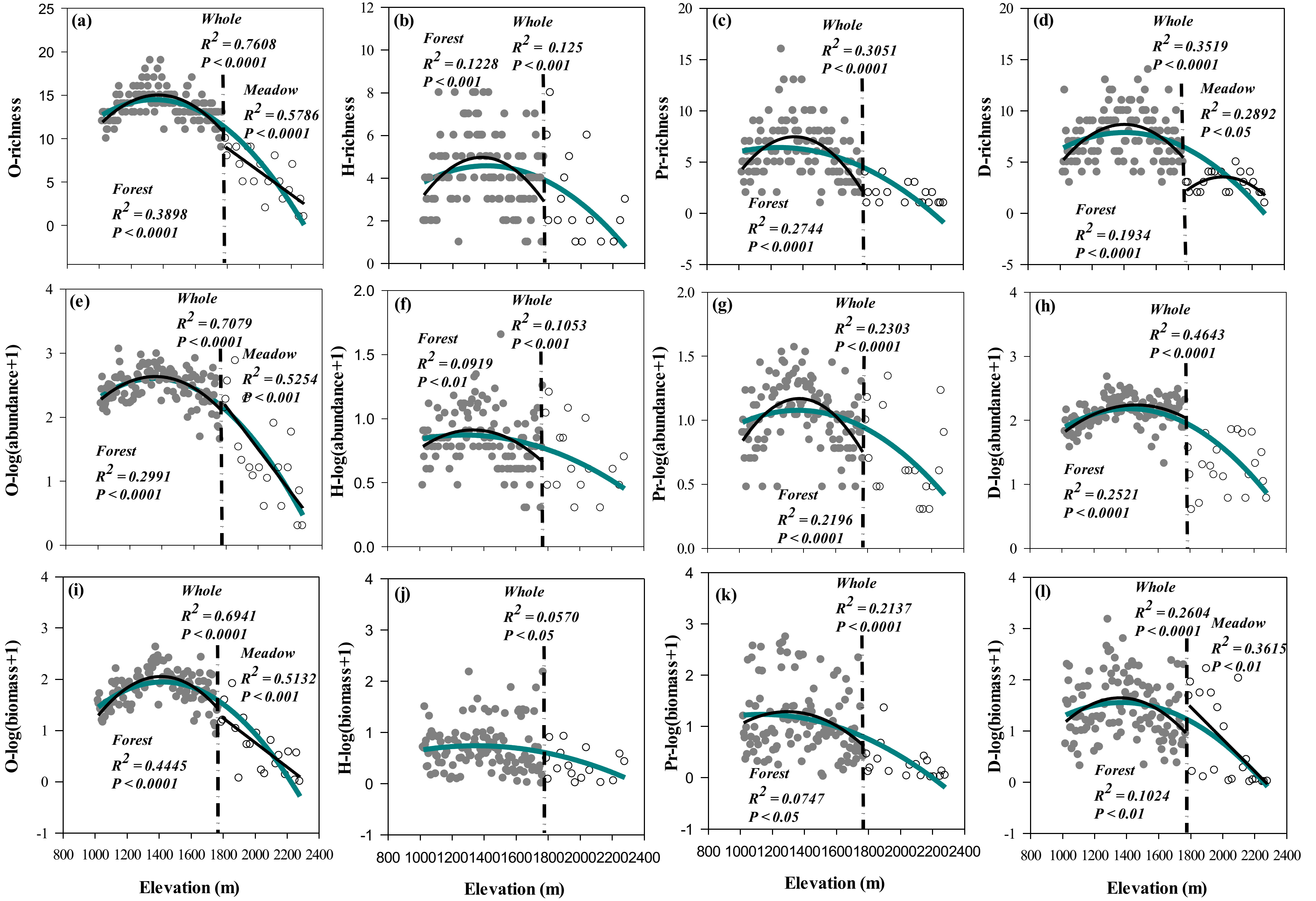

Fig. 1. The richness, abundance, and biomass patterns of litter invertebrates in different feeding guilds along the elevational gradient in Dongling Mountain, China. O, omnivores; H, herbivores; Pr, predators; D, detritivores. Bold dark cyan lines indicate the regression line from a linear model ($P < 0.05$) for the whole elevational gradient. Black lines indicate the regression lines from a linear models ($P < 0.05$) below and above the treeline, respectively. Vertical dashed lines represent the treeline. Grey circles represent data observed in forest below the treeline. White circles represent data observed in meadow above the treeline. (a), (b), (c), and (d) represent the richness patterns of omnivores (O), herbivores (H), predators (Pr), and detritivores (D) along the elevational gradient, respectively; (e), (f), (g), (h) represent the log(abundance+1) patterns of omnivores (O), herbivores (H), predators (Pr), and detritivores (D) along the elevational gradient, respectively; (i), (j), (k), (l) represent the log(biomass+1) patterns of omnivores (O), herbivores (H), predators (Pr), and detritivores (D), respectively.

Table 2
Richness, abundance, and biomass correlation between different feeding guilds of litter invertebrates. Lower triangular matrix represents the Pearson correlations between different functional groups in the forest, while the upper triangular matrix represents those in meadow. The table only showed the correlation coefficients which passed the significant test ($P < 0.05$). O, omnivores; H, herbivores; Pr, predators; D, detritivores.

Richness	O	H	Pr	D	Abundance	O	H	Pr	D	Biomass	O	H	Pr	D
O	–	–	0.51	–	O	–	–	–	–	O	–	–	–	–
H	0.34	–	–	–	H	0.27	–	–	–	H	–	–	–	–
Pr	0.42	0.29	–	–	Pr	0.47	0.26	–	–	Pr	0.26	–	–	–
D	0.3	0.2	0.36	–	D	0.63	0.23	0.34	–	D	0.36	–	–	–

ratios (soil chemical property). The richness and biomass of predators were positively related to sand% (soil physical property), whereas abundance was positively correlated with the sampling temperature (climate). The richness of detritivores was negatively correlated with soil bulk density (soil physical property), whereas abundance was positively correlated with herb cover versus biomass with litter thickness (productivity).

Variance partitioning showed that the environmental predictors in the forest (Fig. 2), independent of elevation (included in the final model), accounted for most of the richness, abundance, and biomass in omnivores, predators, and detritivores. Elevation alone accounted for most of the richness and abundance of herbivores. In the meadow, the shared effects of environmental predictors and elevation accounted for most of the richness, abundance, and biomass of omnivores as well as for the biomass variance of detritivores. Environmental predictors accounted for most of the richness and abundance of herbivores, predators, and detritivores. In total, the unexplained variance in the forest was higher than in the meadow.

4. Discussion

4.1. Elevational richness, abundance, and biomass patterns of litter invertebrates in different feeding guilds across the treeline

We found that omnivores were the most dominant litter invertebrates in biomass as well as in richness and abundance (Fig. 1a,e,i). These results agree with other studies that high omnivory in trophic levels is most dominant in the soil communities (Digel et al., 2014). Consistent with previous studies in most biota (Rahbek, 1995; Rahbek, 2005), all feeding guilds showed hump-shaped patterns along the entire elevational gradient. However, when we conducted further analyses we found that these patterns were mainly driven by the forest gradient, especially for herbivores (Fig. 1b,f,g) and predators (Fig. 1e,g,k), which showed no patterns along the meadow gradient. This was contrary to previous results that herbivores should follow the patterns of plant richness because of their higher levels of dietary specialization than members of other feeding guilds (Maraun et al., 2003). Although the richness and abundance of herbivores was correlated with the herbaceous richness, herbivore diversity may have been more driven by plant identity than richness per se (Schallhart et al., 2012). Predators occupy higher trophic levels of the soil food web (Scheu and Falca, 2000), which leads to the decoupling of the relationships with the other feeding guilds in local habitats. Omnivore richness, abundance, and biomass declined monotonically in the meadow, which suggests that omnivores contributed to all the decreasing patterns of litter invertebrates along the meadow elevational gradient (Xu et al., 2017). Interestingly, there was an obvious break in the richness of detritivores at the treeline. A hump-shaped pattern was found above the treeline, with the same trends as below the treeline. In line with previous studies (David and Handa, 2010), this result suggests detritivores are more sensitive to environmental change than the other feeding guilds. Considering that detritivores can quickly colonize in the early succession stages (Scheu and Schulz, 1996), we infer that the richness pattern break of detritivores at the treeline may have been caused by their faster locomotivity when vegetation types abruptly changed.

Our results showed that the richness, abundance, and biomass of feeding guilds showed similar hump-shaped elevational patterns in the forest but diverse elevational patterns in the meadow. Compared with the previous study (Xu et al., 2017), we found that all feeding guilds contributed to the humped-shaped elevational patterns of the whole litter invertebrate community in the forest but the declining patterns in the meadow were mainly driven by omnivores. The breaks of elevational richness and abundance patterns at the treeline (Xu et al., 2017) were mainly caused by herbivores, predators, and detritivores. These results suggest that elevational patterns of multiple feeding guilds (such as herbivores and predators) will be masked by those of a few dominant feeding guilds (omnivores) when investigating elevational patterns based on the entire litter invertebrate communities.

4.2. Relationships of litter invertebrates between different feeding guilds at two contrasting ecosystems

Previous studies have suggested that considerable functional redundancy may exist in soil food webs (Lawton et al., 1996), which is more likely to occur when faunal groups are diverse (Bardgett, 2002). Forest is thought to support more redundant species than meadow, and we thus supposed that the trophic interactions were weaker in the forest compared with that in the meadow. Contrary to our expectations, the richness and abundance of all feeding guilds were significantly positively correlated to each other in the forest but not in the meadow (Table 2). This means that the feeding guilds may have been more connected with each other in the forest than in the meadow. Trophic interactions in litter invertebrates may be more compact and less redundant (Digel et al., 2014) than previously thought in forest. One possible reason is that the dominant forest type *Quercus* in our study system showed little change below the treeline, and, thus provided a relatively constant resource input across the forest elevational gradient to the soil food web. In line with a former study (Veen et al., 2017), our results also support that the connections between functional group levels in the forest may have been more than those in the meadow. Another reason maybe that in the more fertile and stable forest, nutrient cycling and energy transfer between different trophic levels was less conservative (bacterial-mediated channels) than in the meadow and linked to tighter connections (De Long et al., 2016) and higher energy use efficiency (Wardle et al., 2004) between different feeding guilds of litter invertebrates. The coordination differences between different feeding guilds in the forest and meadow elevational gradients suggest that observed community response within one ecosystem is not necessarily predictive for that of other ecosystems (Kardol et al., 2005). Understanding the relationships between feeding guilds under different stress environmental gradients will have implications for food web modeling in the context of global change. However, we still need more direct evidence to prove this inference by using stable isotopes ($^{13}C/^{15}N$) measurements of the consumer-prey interactions of soil food webs.

4.3. Associations of environmental correlates with litter invertebrates in different feeding guilds across the treeline

Compared with the heterogeneity, productivity (represented by litter thickness in Table 3) in our study was more correlated with elevational richness and the abundance distribution of litter

Table 3
Environmental variables included in the final models to explain the elevational variation in richness, abundance, and biomass of different feeding guilds of litter invertebrates.

Response variable	FOREST			MEADOW		
	R^2	Hypotheses involved	More important variables (beta weights)	R^2	Hypotheses involved	More important variables (beta weights)
O-richness	0.389	**Productivity/** Heterogeneity/Soils 1	**BASEA(0.236), LITTERTH(0.149),** HERBRICH(-0.216), *TSRICH^2(-0.207)*, SILT(-0.119)	0.497	**Climate/** Soils 1	**MAT(0.603),** CONDUN(-0.454)
O-abundance	0.333	**Heterogeneity/** Productivity	***TSRICH^2(-0.248), HERBRICH^2(-0.225),*** BASEA(0.245)	0.619	**Climate**	**MAT(0.682)**
O-biomass	0.357	**Productivity**	**LITTERTH(0.5), BASEA(0.241)**	0.499	**Soils 1**	**CONDUN(-0.511)**
H-richness	0.266	**Climate/** Heterogeneity	**MAP(0.531),** *TSRICH^2(-0.205)*	0.301	**Heterogeneity**	***HERBRICH^2(0.685)***
H-abundance	0.198	**Climate/** Heterogeneity	**MAP(0.322),** *TSRICH^2(-0.175)*	0.047	**Heterogeneity/** Soils 1	***HERBRICH^2(0.455),*** MOISTURE(-0.43)
H-biomass	0.046	**Soils 2**	**pH(-0.177)**	0.315	**Soils 2/** Heterogeneity	**N(-0.754), TP(0.645), CPratio(0.625),** *HERBRICH^2(0.413)*
Pr-richness	0.444	**Productivity/** Soils 1/Heterogeneity/ Soils 2	**LITTERTH(0.412),** BULKDEN(0.387), HERBRICH(-0.223), CNratio(0.159)	0.592	**Soils 1/** Productivity	**SAND(0.779),** HERBCOV(0.735)
Pr-abundance	0.34	**Productivity/** Climate/Soils 1	**LITTERTH(0.448),** MAT(-0.211), BULKDEN(0.209)	0.628	**Climate**	**TINS(0.992)**
Pr-biomass	0.199	**Soils 1/** Heterogeneity	**BULKDEN(0.461), MOISTURE(0.253), SAND(0.144),** HERBRICH(-0.218)	0.549	**Soils 1/** Productivity/ Heterogeneity	**SAND(0.676),** HERBCOV(0.609), HERBRICH(-0.434)
D-richness	0.299	**Productivity/** Soils 1/Heterogeneity	**LITTERTH(0.283), WOODYCOV(0.19),** CONDUN(0.266), *TSRICH^2(-0.201)*	0.548	**Soils 1/** Climate/Heterogeneity	**BULKDEN(-0.457),** MAT(0.438), *HERBRICH^2(-0.377)*
D-abundance	0.31	**Climate/** Heterogeneity/Productivity/ Soils 1	**MAP(0.916), TVAR(0.796), TINS(-0.255),** TSRICH(0.268), BASEA(0.236), MOISTURE(0.141)	0.329	**Productivity/** Climate	**HERBCOV(0.487),** TVAR(-0.381)
D-biomass	0.276	**Soils 1/** Productivity	**MOISTURE(0.418), BULKDEN(0.25), CONDUN(0.133),** LITTERTH(0.232)	0.492	**Productivity/** Soils 2	**LITTERTH(0.471),** CPratio(0.357)

O, omnivores; H, herbivores; Pr, predators; D, detritivores. BASEA, basal area; BULKDEN, bulk density; CONDUN, conductivity; HERBCOV, herbaceous plant coverage; HERBRICH, herbaceous plant richness; LITTERTH, litter thickness; MAP, mean annual precipitation; MAT, mean annual temperature; TINS, the instant temperature during the sampling; TP, total phosphorous content; TSRICH, woody plant (including the tree layer and the shrub layer) richness; TVAR, mean annual temperature range; WOODYCOV, woody plant (including the tree layer and the shrub layer) coverage; Soils 1, soil physical property; Soils 2, soil chemical property. Bold font is used to highlight the single hypothesis most supported by our data.

invertebrates for omnivores, predators, and detritivores below the treeline, which is consistent with previous studies on insects (Woodcock and Pywell, 2010). This result confirms that production was not only the dominant predictor for an entire litter invertebrate community (Xu et al., 2017) but may have also played a significant role across several trophic levels. More productivity means more available energy and resources for litter invertebrates and supports more diverse soil communities and total biomass in different feeding guilds (Scherber et al., 2014). Woody or herbaceous richness was also selected in the final environmental model with lower weights than litter thickness or basal area, which suggests the secondary importance of resource heterogeneity in driving richness distribution patterns (Field et al., 2009). Above the treeline, mean annual temperature (MAT) was most correlated with omnivores. Temperature may directly affect the metabolic rates at which organisms take up, transform and expend energy and materials (Brown et al., 2004) and indirectly affect the net nutrient mineralization and nitrification rates (Sveinbjornsson et al., 1995) to control food resource availability (Davidson and Janssens, 2006; Fierer et al., 2005) for omnivores in a disproportionate way in meadows. Soil physical properties, which replaced productivity as the dominant variables, correlated with predators and detritivores, with sand% positively related to predators versus a negative relation of bulk density to detritivores. We can infer that when an abiotic environment becomes more harsher with increasing elevation in a meadow, the shelter in soil for refuge for predators and detritivores in litter invertebrates becomes much more important than the other biotic or abiotic factors. Another possible reason is that predators and detritivores often have hard exoskeleton and bigger body size.

Differently than the other feeding guilds, the richness and abundance of herbivores was most correlated with mean annual precipitation (MAP) and woody richness in the forest, in contrast to that of herbaceous richness in the meadow. We can infer that herbivores in a meadow are more constrained by direct food resource quality when water stress is alleviated. Soil P content was positively correlated with the biomass of herbivores in the meadow, whereas soil total N content was negatively correlated. This result may suggest that the production of herbivores may have benefited from the availability of phosphorus resources in the meadow, which supports the growth rate hypothesis (the higher the phosphorus availability in the soil, the higher the biomass of large-bodied invertebrates) in line with previous studies in grassland food webs (Mulder and Elser, 2009). Our results also suggest that herbivores in the meadow had been more P-based than previously thought N-based food quality constraints (Masters et al., 1993) with increasing elevation. There may exist other factors that we did not measure, such as chemical deterrents, which also strongly affect herbivore diet choice (Schallhart et al., 2012). Consequently, the unexpected negative correlation between herbivore biomass and N content in this study should be explained with caution. The present study uses the work of Xu et al. (2017) but focuses on the litter invertebrate community, differentiating into different feeding guilds to explore the elevational richness/abundance/biomass patterns and underlying environmental correlates in the perspective of food web modeling.

The hypothesis discussed above does not exclude other possible mechanisms that underlie elevational diversity patterns of litter invertebrates, such as mid-domain effects (Wang et al., 2011) and the biotic disturbance process (Sundqvist et al., 2013). Note that that one drawback of this study is that the skewed distribution of sampling plots across the treeline (approximately a 6-m interval below the treeline versus a 20-m interval above the treeline). The diversity, heterogeneity, and complexity of litter invertebrates in forest habitat is much more than those in meadow; we surveyed more plots in the forest, which may have somehow affected the absolute value of the model fitting. However, considering that the essence of sampling interval settings is to represent the total target population, this difference will not bias the outcomes of elevational patterns and underlying environmental correlates. Additionally, most statistics in the present study, except for

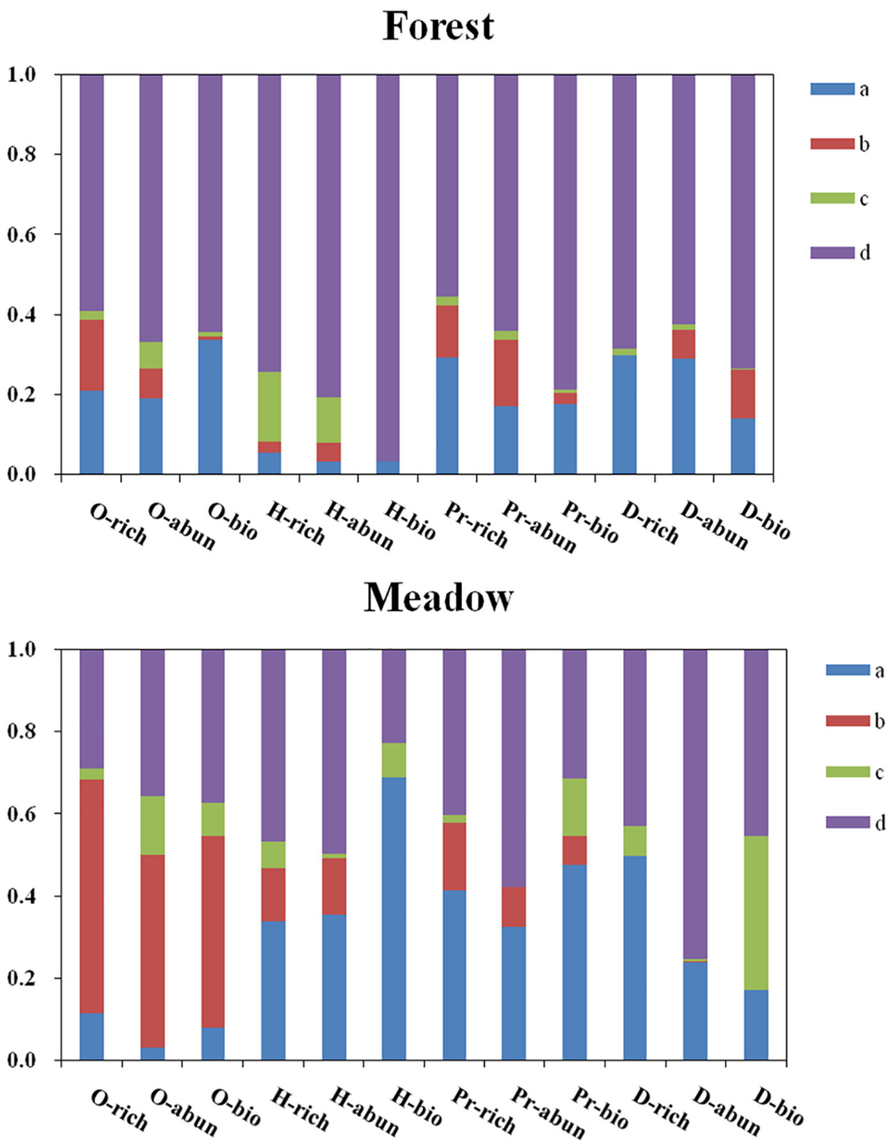

Fig. 2. Variance partitioning of environmental variables in the final model and elevation accounting for the variation of richness, abundance, and biomass of litter invertebrates in different feeding guilds in Dongling Mountain, China. (a) Proportion of environmental predictors accounted for independently of elevation, (b) shared effects of elevation and environmental predictors, (c) spatial variation accounted for by elevation, independently of environmental variables, and (d) unexplained variation. O, omnivores; H, herbivores; Pr, predators; D, detritivores. Richness, abundance, and biomass are abbreviated to "rich", "abun", and "bio", respectively.

the assessment of entire elevational patterns, were separately conducted in the forest elevational gradient below the treeline and the meadow elevational gradient above the treeline. It should also be noted that our family-based separation approach could not rule out the possibility that the trophic position of soil biota may change depending on the forest type (Pfeiffer et al., 2014). However, family-level identification has provided adequate ecological surrogates for species when the focus was on functional guilds in temperate ecosystems (Cardoso et al., 2011). Future studies need to study the spatial distribution patterns of richness, abundance, and biomass of intra- and inter-guilds in litter invertebrates and integrate more environmental hypotheses, as well as higher taxonomic resolutions.

5. Conclusion

Our results suggested that all feeding guilds in litter invertebrates showed hump-shaped patterns in richness, abundance, and biomass along the entire elevational gradient, primarily driven by the variances in forest gradient below the treeline. The feeding guilds were correlated with each other in the forest but not in the meadow. Climate replaced productivity as the main factor that drove the richness and abundance patterns of omnivores above the treeline, whereas heterogeneity replaced climate for herbivores and soil physical properties replaced productivity for predators and detritivores. Our study highlights that the correlated elevational richness, abundance, and biomass patterns of feeding guilds are ecosystem dependent and that underlying environmental correlates shifted at the treeline for most feeding guilds. Comparing elevational richness and abundance and biomass patterns of litter invertebrate feeding guilds and their underlying mechanisms as in the present study, with consideration of different community aspects, could promote a more accurate understanding of the community and of the processes driving belowground food web structures under global change.

Statement of authorship

GRX, KMM, SZ, and YXZ designed the experiment. GRX and SZ did the field investigation of litter invertebrates. YXZ did the plant investigation. GRX identified the invertebrates and measured soil physical and chemical characteristics in lab. Statistical procedures were performed by GRX and SZ. GRX wrote the first draft of the manuscript. All authors contributed substantially to the manuscript, and have no competing interests.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2018.03.212.

References

Bardgett, R.D., 2002. Causes and consequences of biological diversity in soil. Zoology 105, 367–374.

Bardgett, R.D., van der Putten, W.H., 2014. Belowground biodiversity and ecosystem functioning. Nature 515, 505–511.

Beck, J., Mccain, C.M., Axmacher, J.C., Ashton, L.A., Bärtschi, F., Brehm, G., Choi, S.W., Cizek, O., Colwell, R.K., Fiedler, K., 2017. Elevational species richness gradients in a hyperdiverse insect taxon: a global meta-study on geometrid moths. Glob. Ecol. Biogeogr. 26, 412–424.

Blackburn, T.M., Gaston, K.J., 2001. Linking patterns in macroecology. J. Anim. Ecol. 70, 338–352.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M., West, G.B., 2004. Toward a metabolic theory of ecology. Ecology 85, 1771–1789.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference. A Practical Information-Theoretic Approach. Springer-Verlag, New York.

Cardoso, P., Pekar, S., Jocque, R., Coddington, J.A., 2011. Global patterns of guild composition and functional diversity of spiders. PLoS One 6, e21710.

Cornelissen, J.H.C., Perez-Harguindeguy, N., Diaz, S., Grime, J.P., Marzano, B., Cabido, M., Vendramini, F., Cerabolini, B., 1999. Leaf structure and defence control litter decomposition rate across species and life forms in regional floras on two continents. New Phytol. 143, 191–200.

Crotty, F.V., Blackshaw, R.P., Adl, S.M., Inger, R., Murray, P.J., 2014. Divergence of feeding channels within the soil food web determined by ecosystem type. Ecol. Evol. 4, 1–13.

David, J.F., Handa, I.T., 2010. The ecology of saprophagous macroarthropods (millipedes, woodlice) in the context of global change. Biol. Rev. 85, 881–895.

Davidson, E.A., Janssens, I.A., 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature 440, 165–173.

De Long, J.R., Dorrepaal, E., Kardol, P., Nilsson, M.C., Teuber, L.M., Wardle, D.A., 2016. Contrasting responses of soil microbial and nematode communities to warming and plant functional group removal across a post-fire boreal forest successional gradient. Ecosystems 19, 339–355.

Digel, C., Curtsdotter, A., Riede, J., Klarner, B., Brose, U., 2014. Unravelling the complex structure of forest soil food webs: higher omnivory and more trophic levels. Oikos 123, 1157–1172.

Ettema, C.H., Wardle, D.A., 2002. Spatial soil ecology. Trends Ecol. Evol. 17, 177–183.

FAO, F., 1988. UNESCO soil map of the world, revised legend. World Res. Rep. 60, 138.

Field, R., Hawkins, B.A., Cornell, H.V., Currie, D.J., Diniz-Filho, J.A.F., Guegan, J.F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M., Turner, J.R.G., 2009. Spatial species-richness gradients across scales: a meta-analysis. J. Biogeogr. 36, 132–147.

Fierer, N., Craine, J.M., McLauchlan, K., Schimel, J.P., 2005. Litter quality and the temperature sensitivity of decomposition. Ecology 86, 320–326.

Grytnes, J.A., Mccain, C.M., 2007. Elevational trends in biodiversity. Encyclopedia of Biodiversity, pp. 1–8.

Grytnes, J.A., Heegaard, E., Ihlen, P.G., 2006. Species richness of vascular plants, bryophytes, and lichens along an altitudinal gradient in western Norway. Acta Oecol. 29, 241–246.

Haddad, N.M., Crutsinger, G.M., Gross, K., Haarstad, J., Knops, J.M.H., Tilman, D., 2009. Plant species loss decreases arthropod diversity and shifts trophic structure. Ecol. Lett. 12, 1029–1039.

Heiniger, C., Barot, S., Ponge, J.-F., Salmon, S., Meriguet, J., Carmignac, D., Suillerot, M., Dubs, F., 2015. Collembolan preferences for soil and microclimate in forest and pasture communities. Soil Biol. Biochem. 86, 181–192.

Hillstrom, M.L., Lindroth, R.L., 2008. Elevated atmospheric carbon dioxide and ozone alter forest insect abundance and community composition. Insect Conserv. Divers. 1, 233–241.

Hoch, G., Korner, C., 2012. Global patterns of mobile carbon stores in trees at the high-elevation tree line. Glob. Ecol. Biogeogr. 21, 861–871.

Hoeksema, J.D., Lussenhop, J., Teeri, J.A., 2000. Soil nematodes indicate food web responses to elevated atmospheric CO_2. Pedobiologia 44, 725–735.

Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setala, H., Symstad, A.J., Vandermeer, J., Wardle, D.A., 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecol. Monogr. 75, 3–35.

Ibanez, S., 2012. Optimizing size thresholds in a plant-pollinator interaction web: towards a mechanistic understanding of ecological networks. Oecologia 170, 233–242.

Illig, J., Langel, R., Norton, R.A., Scheu, S., Maraun, M., 2005. Where are the decomposers? Uncovering the soil food web of a tropical montane rain forest in southern Ecuador using stable isotopes (N^{15}). J. Trop. Ecol. 21, 589–593.

Jochum, M., Barnes, A.D., Weigelt, P., Ott, D., Rembold, K., Farajallah, A., Brose, U., 2017. Resource stoichiometry and availability modulate species richness and biomass of tropical litter macro-invertebrates. J. Anim. Ecol. 86, 1114–1123.

Kardol, P., Bezemer, T.M., van der Wal, A., van der Putten, W.H., 2005. Successional trajectories of soil nematode and plant communities in a chronosequence of ex-arable lands. Biol. Conserv. 126, 317–327.

Kissling, W.D., Dormann, C.F., Groeneveld, J., Hickler, T., Kuhn, I., McInerny, G.J., Montoya, J.M., Romermann, C., Schiffers, K., Schurr, F.M., Singer, A., Svenning, J.C., Zimmermann, N.E., O'Hara, R.B., 2012. Towards novel approaches to modelling biotic interactions in multispecies assemblages at large spatial extents. J. Biogeogr. 39, 2163–2178.

Lawton, J.H., Bignell, D.E., Bloemers, G.F., Eggleton, P., Hodda, M.E., 1996. Carbon flux and diversity of nematodes and termites in Cameroon forest soils. Biodivers. Conserv. 5, 261–273.

Lee, J.E., Somers, M.J., Chown, S.L., 2012. Density, body size and sex ratio of an indigenous spider along an altitudinal gradient in the sub-Antarctic. Antarct. Sci. 24, 15–22.

Loranger, G., Bandyopadhyaya, I., Razaka, B., Ponge, J.F., 2001. Does soil acidity explain altitudinal sequences in collembolan communities? Soil Biol. Biochem. 33, 381–393.

Maraun, M., Martens, H., Migge, S., Theenhaus, A., Scheu, S., 2003. Adding to 'the enigma of soil animal diversity': fungal feeders and saprophagous soil invertebrates prefer similar food substrates. Eur. J. Soil Biol. 39, 85–95.

Masters, G.J., Brown, V.K., Gange, A.C., 1993. Plant mediated interactions between above- and below-ground insect herbivores. Oikos 66, 148–151.

Mayor, J.R., Sanders, N.J., Classen, A.T., Bardgett, R.D., Clement, J.C., Fajardo, A., Lavorel, S., Sundqvist, M.K., Bahn, M., Chisholm, C., Cieraad, E., Gedalof, Z., Grigulis, K., Kudo, G., Oberski, D.L., Wardle, D.A., 2017. Elevation alters ecosystem properties across temperate treelines globally. Nature 542, 91–95.

McCann, K., 2007. Protecting biostructure. Nature 446, 29.

Mccoy, E.D., 1990. The distribution of insects along elevational gradients. Oikos 58, 313–322.

Minor, M.A., Babenko, A.B., Ermilov, S.G., Khaustov, A.A., Makarova, O.L., 2016. Effects of cushion plants on high-altitude soil microarthropod communities: cushions increase abundance and diversity of mites (Acari), but not springtails (Collembola). Arct. Antarct. Alp. Res. 48, 485–500.

Moreira, F.M.S., Huising, E.J., Bignell, D.E., 2008. A Handbook of Tropical Soil Biology: Sampling and Characterization of Below-Ground Biodiversity. Routledge, London, UK.

Moretti, M., Dias, A.T.C., de Bello, F., Altermatt, F., Chown, S.L., Azcárate, F.M., Bell, J.R., Fournier, B., Hedde, M., Hortal, J., Ibanez, S., Öckinger, E., Sousa, J.P., Ellers, J., Berg, M.P., 2016. Handbook of protocols for standardized measurement of terrestrial invertebrate functional traits. Funct. Ecol. 31, 558–567.

Mulder, C., Elser, J.J., 2009. Soil acidity, ecological stoichiometry and allometric scaling in grassland food webs. Glob. Chang. Biol. 15, 2730–2738.

Mumme, S., Jochum, M., Brose, U., Haneda, N.F., Barnes, A.D., 2015. Functional diversity and stability of litter-invertebrate communities following land-use change in Sumatra, Indonesia. Biol. Conserv. 191, 750–758.

Nielsen, U.N., Osler, G.H.R., van der Wal, R., Campbell, C.D., Burslem, D., 2008. Soil pore volume and the abundance of soil mites in two contrasting habitats. Soil Biol. Biochem. 40, 1538–1541.

Nogues-Bravo, D., Araujo, M.B., Romdal, T., Rahbek, C., 2008. Scale effects and human impact on the elevational species richness gradients. Nature 453, 216–219.

Ott, D., Digel, C., Klarner, B., Maraun, M., Pollierer, M., Rall, B.C., Scheu, S., Seelig, G., Brose, U., 2014. Litter elemental stoichiometry and biomass densities of forest soil invertebrates. Oikos 123, 1212–1223.

Palin, O.F., Eggleton, P., Malhi, Y., Girardin, C.A.J., Rozas-Davila, A., Parr, C.L., 2011. Termite diversity along an Amazon-Andes elevation gradient, Peru. Biotropica 43, 100–107.

Pfeiffer, M., Mezger, D., Dyckmans, J., 2014. Trophic ecology of tropical leaf litter ants (Hymenoptera: Formicidae) - a stable isotope study in four types of Bornean rain forest. Myrmecol. News 19, 31–41.

Rahbek, C., 1995. The elevational gradient of species richness - a uniform pattern. Ecography 18, 200–205.

Rahbek, C., 2005. The role of spatial scale and the perception of large-scale species-richness patterns. Ecol. Lett. 8, 224–239.

Rangel, T.F., Diniz-Filho, J.A.F., Bini, L.M., 2010. SAM: a comprehensive application for spatial analysis in macroecology. Ecography 33, 46–50.

Roder, J., Detsch, F., Otte, I., Appelhans, T., Nauss, T., Peters, M.K., Brandl, R., 2017. Heterogeneous patterns of abundance of epigeic arthropod taxa along a major elevation gradient. Biotropica 49, 217–228.

Root, R.B., 1966. The niche exploitation pattern of the blue-gray gnatcatcher. Ecol. Monogr. 37, 317–350.

Saint-Germain, M., Buddle, C.M., Larrivee, M., Mercado, A., Motchula, T., Reichert, E., Sackett, T.E., Sylvain, Z., Webb, A., 2007. Should biomass be considered more frequently as a currency in terrestrial arthropod community analyses? J. Appl. Ecol. 44, 330–339.

Schallhart, N., Tusch, M.J., Wallinger, C., Staudacher, K., Traugott, M., 2012. Effects of plant identity and diversity on the dietary choice of a soil-living insect herbivore. Ecology 93, 2650–2657.

Scherber, C., Eisenhauer, N., Weisser, W.W., Schmid, B., Voigt, W., Fischer, M., Schulze, E.D., Roscher, C., Weigelt, A., Allan, E., Bessler, H., Bonkowski, M., Buchmann, N., Buscot, F., Clement, L.W., Ebeling, A., Engels, C., Halle, S., Kertscher, I., Klein, A.M., Koller, R., Konig, S., Kowalski, E., Kummer, V., Kuu, A., Lange, M., Lauterbach, D., Middelhoff, C., Migunova, V.D., Milcu, A., Muller, R., Partsch, S., Petermann, J.S., Renker, C., Rottstock, T., Sabais, A., Scheu, S., Schumacher, J., Temperton, V.M., Tscharntke, T., 2010. Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. Nature 468, 553–556.

Scherber, C., Vockenhuber, E., Stark, A., Meyer, H., Tscharntke, T., 2014. Effects of tree and herb biodiversity on Diptera, a hyperdiverse insect order. Oecologia 174, 1387–1400.

Scheu, S., Falca, M., 2000. The soil food web of two beech forests (Fagus sylvatica) of contrasting humus type: stable isotope analysis of a macro- and a mesofauna-dominated community. Oecologia 123, 285–296.

Scheu, S., Schulz, E., 1996. Secondary succession, soil formation and development of a diverse community of oribatids and saprophagous soil macro-invertebrates. Biodivers. Conserv. 5, 235–250.

Schuldt, A., Baruffol, M., Bruelheide, H., Chen, S.M., Chi, X.L., Wall, M., Assmann, T., 2014. Woody plant phylogenetic diversity mediates bottom-up control of arthropod biomass in species-rich forests. Oecologia 176, 171–182.

Stang, M., Klinkhamer, P.G.L., Waser, N.M., Stang, I., van der Meijden, E., 2009. Size-specific interaction patterns and size matching in a plant-pollinator interaction web. Ann. Bot. 103, 1459–1469.

Sundqvist, M.K., Sanders, N.J., Wardle, D.A., 2013. Community and ecosystem responses to elevational gradients: processes, mechanisms, and insights for global change. Annu. Rev. Ecol. Evol. Syst. 44, 261–280.

Sveinbjornsson, B., Davis, J., Abadie, W., Butler, A., 1995. Soil carbon rind nitrogen mineralization at different elevations in the Chugach Mountains of South-Central Alaska, USA. Arct. Alp. Res. 27, 29–37.

Thompson, R.M., Brose, U., Dunne, J.A., Hall, R.O., Hladyz, S., Kitching, R.L., Martinez, N.D., Rantala, H., Romanuk, T.N., Stouffer, D.B., Tylianakis, J.M., 2012. Food webs: reconciling the structure and function of biodiversity. Trends Ecol. Evol. 27, 689–697.

Van der Putten, W.H., Vet, L.E.M., Harvey, J.A., Wackers, F.L., 2001. Linking above- and belowground multitrophic interactions of plants, herbivores, pathogens, and their antagonists. Trends Ecol. Evol. 16, 547–554.

Veen, G.C., Long, J.R.D., Kardol, P., Sundqvist, M.K., Snoek, L.B., Wardle, D.A., 2017. Coordinated responses of soil communities to elevation in three subarctic vegetation types. Oikos 1586–1599.

Voigt, W., Perner, J., Davis, A.J., Eggers, T., Schumacher, J., Bahrmann, R., Fabian, B., Heinrich, W., Kohler, G., Lichter, D., Marstaller, R., Sander, F.W., 2003. Trophic levels are differentially sensitive to climate. Ecology 84, 2444–2453.

Wall, D.H., Nielsen, U.N., Six, J., 2015. Soil biodiversity and human health. Nature 528, 69–76.

Wallwork, J.A., 1976. The Distribution and Diversity of Soil Fauna. Academic Press, New York.

Wang, J., Soininen, J., Zhang, Y., Wang, B., Yang, X., Shen, J., 2011. Contrasting patterns in elevational diversity between microorganisms and macroorganisms. J. Biogeogr. 38, 595–603.

Wardle, D.A., 2006. The influence of biotic interactions on soil biodiversity. Ecol. Lett. 9, 870–886.

Wardle, D.A., Bardgett, R.D., Klironomos, J.N., Setala, H., van der Putten, W.H., Wall, D.H., 2004. Ecological linkages between aboveground and belowground biota. Science 304, 1629–1633.

Werenkraut, V., Ruggiero, A., 2011. Quality of basic data and method to identify shape affect richness-altitude relationships in meta-analysis. Ecology 92, 253–260.

Werenkraut, V., Ruggiero, A., 2014. The richness and abundance of epigaeic mountain beetles in North-Western Patagonia, Argentina: assessment of patterns and environmental correlates. J. Biogeogr. 41, 561–573.

Woodcock, B.A., Pywell, R.F., 2010. Effects of vegetation structure and floristic diversity on detritivore, herbivore and predatory invertebrates within calcareous grasslands. Biodivers. Conserv. 19, 81–95.

Xu, G., Zhang, S., Lin, Y., Ma, K., 2015. Context dependency of the density–body mass relationship in litter invertebrates along an elevational gradient. Soil Biol. Biochem. 88, 323–332.

Xu, G., Lin, Y., Zhang, S., Zhang, Y., Li, G., Ma, K., 2017. Shifting mechanisms of elevational diversity and biomass patterns in soil invertebrates at treeline. Soil Biol. Biochem. 113, 80–88.