Effects of Environment and Space on Species Turnover of Soil Faunas across Multiple Forest Ecosystems in East Asia

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Abstract

Species turnover is fundamental for understanding the mechanisms that influence large-scale species richness patterns. However, the large-scale spatial variation and the causes in soil animal species turnover remain elusive. In addition, the determinants of species turnover depend on the dispersal ability of guilds. In this study, we explored the large-scale patterns of meso-micro soil fauna turnover pattern and the driving factors based on fourteen sampling sites in East Asia. The patterns of soil fauna species turnover increased significantly with increasing latitude differences in East Asia. The environment explained 54.09, 50.62, and 57.34% of the total variance, and spatial factors explained 13.84, 15.91, and 21.04% of the total variance in species composition of overall, phytophage, and predacity faunas, respectively. Meanwhile, the effects of climate factors in environmental processes were stronger than that of soil factors in these three groups. Our results support the hypothesis that the effect of environment processes on soil animal species turnover is more important than the effect of the neutral. Climatic factors explained more variation for turnover of phytophage faunas, but soil and environment factors explained equally for predacity. Our results provide evidence supporting both environmental filtering and dispersal limitation hypotheses on the reginal and population scales. At last, this study has important theoretical significance and applied value in maintaining and promoting soil biodiversity and ecosystem services on the large scale.

Introduction

Soil biodiversity drives complicated ecological processes and plays a crucial role in exerting ecosystem functions and the provision of ecosystem services (Nielsen et al., 2012; Wagg et al., 2014; Geisen et al., 2018). The composition of soil animal communities thus strongly influences ecosystem multifunctionality (Wagg et al., 2014). For instance, soil animal communities may alter microbial activity, litter decomposition, nutrient mineralization, soil respiration, and plant community composition (Bradford et al., 2002; De Deyn et al., 2003; Eisenhauer et al., 2012; Johnston & Sibly, 2018). Consequently, shifts in soil animal community composition could dramatically influence the functioning and stability of terrestrial ecosystems (Sjursen et al., 2005; Suttle et al., 2007; Briones et al., 2009; Eisenhauer et al., 2014; Handa et al., 2014). Yet, little is known about the spatial and environmental factors that shape soil animal communities on a regional and global scale (Johnston & Sibly, 2020). To understand the ecosystem functioning and the mechanism of community composition evolvement, it is necessary to identify the factors that shape the distribution and structure of various soil faunas (Crowther et al., 2019).

Species turnover pattern (or beta diversity) is a basic pattern in biogeography and macroecology (Gaston, 2000), and it provides fundamental insights into mechanisms of community assembly, especially on a large scale (Anderson et al., 2011; Lafage et al., 2015). However, species turnover patterns have received less attention than alpha diversity (Lennon et al., 2001), and measures of species turnover in previous studies

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usually based on single method (Gao et al., 2021). Utilizing different methods to measure the species turnover rates can better avoid the error caused by methods of measurement. Meanwhile, most studies on species turnover have been conducted locally (Kraft et al., 2011; Sasaki & Yoshihara, 2013). A few studies did investigate species turnover on large geographic scales, but they mostly focused on plants and animals. For example, recent studies have demonstrated that dispersal abilities were a key factor for both woody plants and birds in species turnover spatially (Chen et al., 2016; Sreekar et al., 2020). The global biogeography of soil animals has begun to gain attention only recently (Caruso et al., 2005; Dunn et al., 2009; van den Hoogen et al., 2019; Medini et al., 2021). Most of these studies focused on specific soil animal communities. For example, previous studies showed that earthworm community composition is determined by the mobility of the organisms (Medini et al., 2021), oribatid mite by spatial factors (Caruso et al., 2005), termites of Hymenoptera by temperature and precipitation (Dunn et al., 2009), and nematodes by temperature (van den Hoogen et al., 2019). Despite our accumulated knowledge about biogeographic patterns of soil biota, the underlying mechanisms of the distribution patterns remain unexplored (Xu et al., 2020). Particularly, the studies on the patterns of comprehensive taxa species turnover across latitudes are limited.

Environmental filtration and spatial processes have been associated with variations in ecological communities and biodiversity. However, their significance on multiple dimensions of beta diversity has not been fully explored in soil fauna (Li et al., 2020). Several research studies indicated that species coexistence was attributed to different environmental factors, such as habitat heterogeneity (Li et al.,2017), temperatures in different climates (Oliver et al., 2009), and soil nutrients (John et al., 2007). These factors provided species with different resources, time, and space to achieve coexistence as implied by the niche theory (Jia et al., 2015; Escudero & Valladares, 2016). Alternatively, neutral processes stated that species coexistence was resulted from biogeographic barriers and low dispersal abilities (Hubbell, 2001; Jia et al., 2015). Though two different theories, the niche theory and neutral processes actually jointly explained the coexistence of soil animal communities. They just have different roles on corresponding spatial scales (Gao et al., 2014). The underlying environmental controls that shape latitudinal shifts in soil animal communities on a global scale, however, have not been identified (Johnston & Sibly, 2020), especially the mechanisms. Therefore, our study aimed at addressing this knowledge gap and explored the influence of spatial and environmental factors on soil animal species composition across globally distributed sites by synthesizing data of comprehensive taxa of soil animal communities.

The objectives of the current study were: (1) to obtain an integrated analysis of the similarity of soil animal species composition along the latitude in East Asia, (2) to identify the patterns of species turnover along the latitude using two measures of species turnover, and (3) to assess the relative influence of environmental and neutral processes on species turnover of overall and functional forms of soil animals.

Materials and Methods

Study sites

In this study, 14 sampling sites of different climatic zones in East Asia were selected (Figure 1), and they were: the Tahe, Aershan, Changbaishan, Donglingshan, Baotianman, Badagongshan, Tiantongshan, Shimentai, Jianfengling, Xishuangbanna, Guanghwa, Sapporo, Hiroshima, and Yushan. The latitude of the site cross ranges from 18.50° to 52.33°, and the climatic zones include temperate, subtropical, and tropical zones. The vegetation types in the study areas include temperate coniferous and broad-leaved mixed forest temperate deciduous broad-leaved forest, temperate deciduous broad-leaved forests, subtropical evergreen broad-leaved forests, and tropical rain forests. Method of Tullgren was used for the isolation of the soil animals and then the soil animals were identified based on morphology using the same criteria in all samples (Yin et al., 1998; Yin, 2000).

Species and environment variables

In the study, we used data on the species catalog, which was obtained from 14 literatures listed in Table S1 (Huang et al., 2008; Zhang et al., 2007; Han et al., 2015; Xu et al., 2017; Xu et al., 2020; He, 2018; Yi, 2005; Li et al., 2004; Yang et al., 1998; Xiong, 2005; Kwon et al., 2016; Nakamura et al., 1970; Yoshifumi et al.,

1994; Chuan et al., 2003). The 14 sampling sites differed in established time, region, and researchers (Table 1 and 2). The soil fauna identification may vary among plots at family levels. Thus, the order names in the samples were checked based on the *Pictorial Keys to Soil Animals of China* (Yin et al., 1998) and *Catalogue of Life China* (2013). Concurrently, all species were divided into four functional types based on their feeding guilds, as follows, saprozoic, omnivores, phytophage, and predacity (Table S2) (Zhang et al., 2001; Xu et al., 2017).

In each sampling site, soil animals were sampled from litter layer and/or soil cores in multiple seasons (Table 2). The sampling superficial area was 0.73 ± 0.58 m^2 and the sampling volume was 0.071 ± 0.061 m^3 (Table 2), and the sampling quantity was 339 ± 153. Furthermore, the minimum number of soil fauna individuals was 9684 and the maximum was 52673. This way, these samplings can well reflect the profile of the species composition in that particular region, because the total sampling areas were designed to adequately cover both microhabitats and plant species (Basset et al., 2012). Therefore, the effects of sampling difference on large-scale species composition among plots were negligible. Not only that, the 14 scientific studies selected in this paper declareed that the sampling completeness of each study could fully reflect the composition of local soil fauna community.

The longitude and latitude of the samples, climate factors [mean annual precipitation (MAP, mm), mean annual temperature (MAT, °C), mean temperature of the coldest months (MTCM, °C), extreme minimum temperature (EMT, °C)], and soil factors including soil organic carbon (SOC, g/kg), soil bulk density (SBD, kg/m^3), and pH value were analyzed and compared among the samples. Longitude and latitude, climate factors, and soil factors were obtained from National Earth System Science Data Center (http://www.geodata.cn/), Google Earth Engine (earthengine.google.com/), or literature (Table 1 and 3).

Measurement of species turnover rate

Species turnover rate is the rate of dissimilarity among species composition across all possible plot pairs along the spatial or environmental gradient. The slope of the relationship between the species turnover and environmental divergence measures species turnover rate. Jaccard's index (β_j; Jaccard et al., 1912) and SØrenson's index (β_s; SØrenson et al., 1948) were used to measure turnover rate of species composition. β_j and β_s are two widely employed indices, which only consider presence/non-presence of species, are independent of α-diversity (Jost et al., 2007). β_j and β_s are calculated following the equations:

$$\beta_j = 1 - c/(a+b+c) = (a+b)/(a+b+c)$$

$$\beta_s = 1 - 2c/(a+b+2c) = (a+b)/(a+b+2c)$$

where a and b are the numbers of species only occurring in the focal and neighboring plots, respectively, and c is the number occurring in both.

Data analysis

We used detrended correspondence analysis (DCA) for the ordination of samples. DCA is an effective method in community analysis. In our study, we conducted DCA using a site-order matrix with relative abundance data to analyze the similarity of order compositions among samples. Kruskal-Wallis method was used for analysis differences in the richness of soil faunas in the three climatic regions.

We performed a redundancy analysis (RDA) based variation partitioning analysis to assess the relative effects of environmental and spatial variables on soil fauna community composition. Before the RDA, the environmental variables with high variance inflation factor (VIF) >10 were eliminated to avoid collinearity among factors (Singh et al., 2019). The importance of environmental and spatial variables in explaining order compositions was determined by an RDA analysis using Monte Carlo permutation tests (999 unrestricted permutations) followed by forward selection to remove the non-significant variables from each of the explanatory sets. The "envfit" function in the R software with "vegan" package was used to test the

significance of each environmental factor and orders distribution (Oksanen et al., 2007). The pH value results were not significant in overall, phytophage, and predacity species composition, so the pH value was excluded in the subsequent analysis.

For environmental variables, climate and soil factors (MAP, MAT, MTCM, EMT, SOC, and SBD) were used to determine the environmental divergence between pairs of sampling sites. All environmental variables were normalized as: $x' = (x - \text{mean}(x)) / \text{standard deviation} (x)$, where x is a variable. Differences of latitude values (Table 1) of the sampling sites were used to obtain the spatial variable as a response variable. Relationships between turnover rate of order compositions and environmental and spatial variables were determined with linear regression. We used the dissimilarity coefficient (β_j and β_s) as the response variable and three sets of explanatory variables which included climate variables (MAP, MAT, MTCM, and EMT), soil factors (SOC, and SBD) and spatial variables (geographical co-ordinates for sampling sites), respectively. Where necessary, values were log $(x + 1)$ transformed in order to meet assumptions of normality of residuals.

To further evaluate the relative importance of each environmental variable and spatial distance on the order turnover rates, we used a Partial RDA (pRDA) approach. This method can analyze the effects of pivot variables and covariables on order distributions respectively (Lososová er al., 2004). Partial RDA analysis divided the variance in order turnover index into eight parts, which were pure spatial effects, pure climate effects, pure soil effects, spatially structured climate effects, spatially structured soil effects, climatological soil effects, spatially structured environmental effects, and the unexplained part.

All statistical analyses were carried out with R v.3.4.3 (R Core Development Team, 2017). DCA and PCA were performed using the "vegan" package (Oksanenetal et al., 2007).

Results

Structural characteristics of soil fauna community

A total of 49 orders were included in the final dataset, including 14 classes in 4 phyla. We classified all sites into three climate types based on their geographic locations, thermal characteristics, and water availability, as follows: temperate, subtropical, and tropical. The vegetation types include temperate coniferous and broad-leaved mixed forest, temperate deciduous broad-leaved forest, subtropical evergreen broad-leaved forest, and tropical rain forest (Figure 1). In general, the number of orders declined significantly with increasing latitude of overall orders, phytophage, and predacity faunas (Figure 1). The soil fauna diversity in the temperate zone was significantly different from that in the other two climatic zones ($?^2 = 7.582, p = 0.02$, Figure 1). The difference of phytophage ($?^2 = 0.352$, $p = 0.839$, Figure 1) and predacity ($?^2 = 1.040$, $p = 0.595$, Figure 1) orders were not significant in the three climatic regions (Figure S1). Among the 14 sites being studied, the Jianfengling site belonged to the tropical rain forest, showed the highest among all plots (Overall: 33, phytophage: 9, predacity: 7). In contrast, the Aershan site, which belonged to the coniferous and broad-leaved mixed forests in cold temperate zones, showed the lowest species diversity among all plots (Overall: 14, phytophage: 3, predacity: 3; Figure 1).

DCA analysis was conducted to show plot ordinations (Figure 2). The highest similarity in order compositions was observed between Aershan and Changbaishan. Further, Sapporo and Tahe were observed with similar order compositions with Aershan and Changbaishan, as all of these four sites were in high-latitude temperate regions. Analogously, high similarities in order compositions were observed among the Tiantongshan, Badagongshan, Xishuangbanna, and Jianfengling sites, which were all located in low-latitudes subtropical and tropical regions.

The Monte Carlo permutation test showed that the total effects of Latitude, MAT, MTCM, EMT, and SOC reached a significant level on overall orders, phytophage, and predacity soil fauna composition (Table 4). The results of RDA ordination showed that seven variables of spatial and environmental factors can explain 31.7%, 36.0%, and 42.4% variation of total information of soil animal composition at overall orders, phytophage, and predacity, respectively (Figure 3).Specifically, the 1st ordination axis explains 18.7%, 20.9%, and 26.4% variation information of overall orders, phytophage, and predacity, respectively, and the 2nd

ordination axis explains 13%, 15.1%, and 16% variation information, respectively. Soil fauna community was observed to be strongly affected by spatial and environmental factors (Table 4). Community composition differed significantly in the different latitudes ($R^2 = 0.519$, $p = 0.023$). Variations in fauna orders showed a strong response to soil physicochemical properties ($p = 0.004$, Figure 3a) and temperature ($p = 0.033$, Figure 3a). The dominant Lumbricida belonging to Oligochaeta exhibited a positive relationship with SOC or latitude but a negative relationship with SBD, MAP, MAT, MTCM, or EMT values (Figure 3a). However, for Malacostraca, the dominant Isopoda showed a negative relationship with SOC or Latitude, but a positive relationship with MAT, MTCM, or EMT (Figure 3a). The phytophage Mesogastropoda belonging to Gastropoda was positively correlated with SOC and negatively correlated with SBD (Figure 3b), whereas the predacity Isoptera belonging to Insecta was observed as the opposite (Figure 3c).

Patterns of orders turnover

Both βj and βs increased significantly with the increasing latitude difference of overall orders (slop = 0.025, $R^2 = 0.057$, $p < 0.05$; and slop = 0.019, $R^2 = 0.051$, $p < 0.05$, Figure 4a; Table 5), phytophage faunas (slop = 0.035, $R^2 = 0.046$, $p < 0.05$; and slop = 0.036, $R^2 = 0.053$, $p < 0.05$, Figure 4b; Table 5), and predacity faunas (slop = 0.054, $R^2 = 0.12$, $p < 0.001$; and slop = 0.039, $R^2 = 0.12$, $p < 0.001$, Figure 4c; Table 5), respectively. Both βj and βs increased significantly with the increase of EMT and SOC for overall orders (Figure 5d and 4d), phytophage (Figure 5e and 4e), and predacity (Figure 5f and 4f) faunas. With the increase of MAT and MTCM, both βj and βs were observed to be increased for phytophage (Figure 5b and 5h) and predacity (Figure 5c and 5i) faunas, whereas βj and βs of only predacity faunas were observed to be increased significantly with the increasing MAP and SBD (Figure 5l and 4i; Table 5). Though βj and βs were increased with increasing latitude difference and SOC, the orders turnover rate of phytophage faunas was less than that of predacity faunas (Table 5).

Determinants of species turnover

Four climate factors, two soil factors, and latitude factors were used to assess the effects of the environment and space. Partial RDA analysis indicated that the effects of environment and space were 54.09% and 13.84%, respectively, for overall faunas (Figure 6). The effects of pure climate on soil fauna composition were the strongest (31.27%), followed by pure soil factors (15.78%) and pure spatial factors (8.31%) for overall fauna order compositions (Figure 6a). Therefore, environmental factors and primarily climate, explained most of the variation in overall soil fauna order compositions.

For phytophage faunas, the effects of pure climate were 29.95%, pure soil were 9.65%, and pure spatial factors were 6.59% (Figure 6b). The effects of pure climatic factors were stronger than those of pure soil and pure spatial on soil animal composition, whereas for predacity faunas, the effects of pure climatic and soil factors were basically the same (Figure 6c). Moreover, the effects of pure climate factors on soil fauna order compositions for predacity faunas were the lowest, and the effects of pure soil and the spatially structured climatic factors were the highest (Figure 6).

Discussion

Large number of soil animal study sites have been established in different regions worldwide (Yin et al., 2010; Wu et al., 2011), and many scholars have studied soil fauna on their ecological function (Lubbers et al., 2020) and soil animal coexistence mechanisms (Stefanie et al., 2015; Guo et al., 2018). However, most of these studies were on reginal or population scales (Marchen et al., 2015; Song et al., 2017; Phillips et al., 2019). There is a lack of studies that analyze communities with broad ranges of taxa on large scales. Various ecosystems worldwide are interconnected. Thus, integrating comparative large-scale analyses could better reveal the laws of soil fauna community distributions and species coexistence mechanisms.

Soil fauna community distributions

In this study, the comparative analysis was conducted on the order composition similarities of 14 forest sites in East Asia. As expected, smaller distances between the sites tended to increase similarity in species composition (Figure 2). Order richness was observed to be decreased with increasing latitude (Figure 1). This

was consistent with most research findings that lower latitudes provide more available resources (Convey, 2013; Johnston & Sibly, 2018). Decaëns (2010) pointed to an enhanced efficiency of mutualism under tropical climates as a possible reason for a latitudinal gradient in soil animal communities. However, the results of this study found that the total richness of soil animals in temperate zones was significantly higher than that in tropical and subtropical zones, which was in line with the results of the non-linear shifts in soil animal community with latitude studied by Petersen and Luxton (1982). Total soil animal biomass declined from temperate ecosystems (forests and grass-lands) towards both arctic and tropical ecosystems and were accompanied by shifts in soil animal community composition (Alice et al., 2020). For instance, the biomass of smaller soil animal groups (Nematoda, Collembola, Enchytraeidae, and Acari) decreased in tropical ecosystems comparing to temperate ecosystems (Petersen 1982; Johnston & Sibly, 2020). This could be resulted from different tolerance of the diverse soil faunas to climate, especially temperature.

Based on the 14 sites we studied, the patterns of order turnover increased significantly with increasing latitude differences for β_j and β_s of overall orders, phytophage, and predacity faunas, respectively (Figure 4). These results were consistent with those obtained in previous studies (Abrahamczyk et al., 2011; Ulrich et al., 2012; Andersen et al., 2015). The reasons for the increase in order turnover rate with increasing latitude differences could be complicated. Among the reasons, latitudinal gradients in climatic tolerance and sampling effect of the species pool have been mostly reported (Dunck et al., 2016; Kent et al., 2020). The hypothesis of latitudinal gradients in climatic tolerance claims that species are more climatically tolerant in high than in low latitudes (Chen et al., 2016). Lower climatic tolerance may further lead to narrower niche breadths in tropical than in temperate mountains, thereby decreasing the likelihood of co-occurrence of different species and increasing the species turnover rate (Janion-Scheepers et al., 2019; Kent et al., 2020).

Driving forces of soil fauna community construction

Recent global syntheses of soil communities have identified contrasting environmental controls on the distribution and abundance of soil animal groups (Alice et al., 2020). Our research shows that soil texture and temperature, especially the lowest temperature in the region, were important factors in shaping the distribution pattern of soil animals in East Asia. Similar conclusions were drawn from other studies. For example, global earthworm communities were observed to be strongly impacted by climatic variables (Phillips et al. 2019), and nematode abundances were observed to be increased with an increase in SOC content (Van Den Hoogen et al., 2019). However, these soil animal communities were also found to be influenced by other additional factors. For instance, soil acidity was found to influence global earthworm communities across natural and managed ecosystems, with higher species richness at intermediate soil pH levels (Johnston & Sibly, 2018). Nematode abundances were found to be decreased with increasing soil pH on a global scale (Van Den Hoogen et al., 2019). And interestingly termites were influenced by climatic factors on a regional scale, with termite diversity being highest in moist lowland tropical rainforest ecosystems (Jones & Eggleton, 2010).

Relationships of soil animal groups on a global scale broadly follow those identified for soil fungi and bacteria (Johnston & Sibly, 2020). On the global scale, climatic factors were found as the main factors affecting the diversity of soil fungi in global natural ecosystems (Tedersoo et al., 2014), and soil organic carbon level was found as the main factor affecting fungal diversity (Liu et al., 2015) on regional scales (Northeast China). The changes of temperature and SOC were further expected to cause microbial community composition shifts between fungal and bacterial dominance, leading to various trophic transfer efficiency to their soil animal consumers (Carrillo et al., 2016). The research results showed that SOC, temperature, especially the extreme minimum temperature are environmental factors that affected the overall distribution of soil animals in East Asia. Our study generalized these results to entire soil animal communities, and showed a dominance of small soil animals (e.g., Nematoda, Acari, Collembola) in high-latitude with low temperature and higher SOC contents, and greater abundances of larger soil animals (e.g., Chilopoda, Coleoptera) at mid- to low latitudes in more neutral temperature with lower SOC contents. Nevertheless, our research was inconsistent with the global research results of species distribution dominated by pH (Johnston & Sibly, 2020). The reason for this inconsistency may be because numerous taxa showed hemispheric asymmetries in latitudinal

diversity gradients: trees (Burns, 2007), mammals (Gaston et al., 1995), termites (Eggleton et al., 1994), birds (Blackburn & Gaston, 1996), spiders (Platnick & Norman, 1991), ants (Dunn et al., 2009) and triatomids (Rodriguero & Gorla, 2004). Simultaneously, predacity soil animals are more susceptible to environmental impacts than phytophage animals (Roslin et al., 2017), which may lead to different distribution pattern of different functional soil animals in East Asia. This may be attributed to the relatively broad ecological niches of species with higher trophic levels, leading to multiple environmental requirements and adaptations (Chen et al., 2014; Turney & Buddle, 2016).

Ecological processes of soil fauna community construction

Most ecological patterns and processes in nature are scale-dependent (Gao et al., 2014; Widenfalk et al., 2015; Gao et al., 2021), that is, their community patterns and construction mechanisms could be different under different spatial scale conditions (Chase & Leibold, 2002), and may be simultaneously controlled by processes from multiple scales (Levin, 1992, Guo er al., 2018). Locally, pure spatial variables were important in regulating species composition, whereas the spatially structured environmental factors contributed most at regional scale at the northeast China (Gao et al., 2021). Our results supported the hypothesis that the effect of environmental processes on order turnover of soil fauna in East Asia is more important than that of neutral processes. Our study area and the obtained species taxon were different with the study of Gao et al. (2021). Therefore, our results were not entirely consistent with those of Gao's.

The mechanism causing patterns of soil animal communities in East Asia was driven by environmental processes, but the driving paths of herbivorous and predatory animal communities may be different (Roslin et al., 2017). This study showed that the effect of environmental processes was more important than neutral processes for phytophage and predacity faunas, and that the effects of the latitude difference for predacity were minimal. The active dispersal abilities of soil animals separated by a Tullgren along the soil matrix was generally very limited (Gao et al., 2018). This may weaken the influence of the neutral process. In contrast, soil animals were sensitive to environmental changes (Fu et al., 2009; Wu, 2011). Thus, soil animals were more affected by environmental processes.

These results contrasted with the findings obtained by Zhang (2016) and Gao (2018), who determined that neutral processes explained more variation for soil faunas. This discrepancy may result partly from the use of spatial extents and species variables in the two studies. Zhang (2016) and Gao (2018) focused only on northeast of China and the two soil animal groups of beetles and mites. By comparison, our study covered 14 research samples and three temperature belts in East Asia. In particular, our taxon included almost all soil animal groups. Thus, we concluded that on a large scale, environmental processes explained more variation for turnover of soil faunas.

The effects of climate as an environmental factor on phytophages was greater than that of soil, but the effects of climate and soil factors in predators was basically the same. Climate, mainly temperature, drive the species conversion of forest trees and shrubs in East Asia (Chen et al., 2016), led to changes in the food resources of phytophagous. Therefore, the influence of climate was observed to be greater than that of soil as environmental driving factors. For predatory animals, the biotic interaction (predation behavior) strength increases towards the equator may cause the expansion of the resources available to the predator, leading to the expansion of the niche (Roslin et al., 2017). The width of niche could be restricted by more environmental factors, such as climate and soil. Therefore, climate factors and soil factors were almost equally important in the construction of soil animal communities in East Asia.

Finally, our study used order-level identification to ensure the consistency of soil fauna taxon in all sites in East Asia. Ponge and Salmon's (2013) study showed that environmental filtering or species sorting culminated at the family level, and were obscured by convergent evolution and co-adaptation at higher taxonomic levels. High family-level diversity was commonly associated with a high structural or trait diversity (Terlizzi et al., 2009; Zou et al., 2020). Order-level classification was adequate for the needs of our research, because this study only focused on the presence/absence of information on species instead of specific traits of species. However, biological interactions processes, such as nutritional level and food web structure,

phylogeny, and functional traits are the important factors that are often ignored in community ecology studies. Therefore, future research should consider more and better biological factors and distinguish the effects of neutral and environmental processes on a community assembly.

Conclusion

The patterns of soil fauna species turnover increased significantly with increasing latitude and environment differences in East Asia. Our results supported the hypothesis that the effect of environmental processes was more important than the effect of neutral processes on species turnover of soil faunas. However, the mechanisms underlying such patterns of species turnover may differ among phytophage and predacity faunas. Environmental processes explained more variation for turnover of both phytophage and predacity species. Climatic factors in environmental processes explained more variation for turnover of phytophage faunas, and soil and environment factors explained the variation equally for the turnover of predacity soil faunas on a large scale. Therefore, phytophage and predacity species with different functional traits and trophic levels should receive different protection strategies in maintaining and promoting soil biodiversity and ecosystem services on a large scale.

AUTHOR CONTRIBUTIONS

Shengyan Ding: Conceptualization (lead). Shunping Ding: review and editing (lead). Peikun Li: writing – original draft (lead); formal analysis (lead); writing – review and editing (equal). Jian Zhang: Software (lead); writing – review and editing (equal). Panpan Zhang: Methodology (lead); writing – review and editing (equal). Zihan Geng: Conceptualization (supporting); Writing – original draft (supporting); Writing – review and editing (equal).

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

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Figure captions:

Figure 1. Locations of 14 sampling sites in East Asia, where TH = Tahe, ARS = Aershan, CBS = Changbaishan, DLS = Donglingshan, BTM = Baotianman, BDGS = Badagongshan, TTS = Tiantongshan, SMT = Shimentai, JFL = Jianfengling, XSBN = Xishuangbanna, GH = Guanghua, SPK = Sapporo, HMA = Hiroshima, and YS = Yushan. The fourteen sites belong to three climate zones, which are Temperate zone (Temp), Subtropical zone (Subt), and Tropical zone (Trop). The graph on the bottom left shows the numbers of overall ($?^2$=7.582, p=0.02), phytophage ($?^2$=0.352, p=0.839), and predacity ($?^2$=1.040, p=0.595) orders in temperate, subtropical, and tropical zone, "a" and "b" represent significant differences. The subset

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of graphs on the bottom right shows the relationship between the number of orders and latitudinal across fourteen sampling sites. Note: "*" indicated p [?] 0.05 and "**" indicated p [?] 0.01.

Figure 2. DCA analysis of soil fauna order compositions among 14 sampling sites in East Asia, where TH = Tahe, ARS = Aershan, CBS = Changbaishan, DLS = Donglingshan, BTM = Baotianman, BDGS = Badagongshan, TTS = Tiantongshan, SMT = Shimentai, JFL = Jianfengling, XSBN = Xishuangbanna, GH = Guanghua, SPK = Sapporo, HMA = Hiroshima, and YS = Yushan.

Figure 3. Ordination diagram for the RDA analysis for soil fauna distribution and environmental factors in East Asia. The (a), (b), and (c) present the overall, phytophage, and predacity soli fauna orders, respectively. The blue and red arrows represent environmental factors and orders, respectively. The red circles, green squares, and blue diamonds represent temperate, subtropical, and tropical zones, respectively. In the graphs, MAT = mean annual temperature, MTCM = mean temperature of the coldest months, EMT= extreme minimum temperature, MAP = mean annual precipitation, SOC= soil organic carbon, and SBD = soil bulk density. Climate factors included MAT, MTCM, EMT, and MAP. Soil factors included SOC and SBD. Order name abbreviations are shown in Table S2. Note: "*" indicated p [?] 0.05 and "**" indicated p [?] 0.01.

Figure 4. Patterns of overall (a), (d), (g), phytophage (b), (e), (h), and predacity fauna (c), (f), (i) in different sampling sites along the latitude and soil factor difference in East Asia. Orange dots and lines represent βj and blue dots and lines represent βs, n = 91; The "*", "**", and "***" represent p [?] 0.05, 0.01, and 0.001, respectively. "NS" indicates not significant. (Note: SOC = soil organic carbon, and SBD = soil bulk density)

Figure 5. Patterns of overall (a), (d), (g), (j), phytophage (b), (e), (h), (k), and predacity fauna (c), (f), (i), (l), in different sampling sites along the environmental difference in East Asia. Orange dots and lines represent βj and blue dots and lines represent βs, n = 91; The "*", "**", and "***" represent p [?] 0.05, 0.01, and 0.001, respectively. "NS" indicates non-significant. (Note: MAT = mean annual temperature, MTCM = mean temperature of the coldest months, EMT = extreme minimum temperature, MAP = mean annual precipitation)

Figure 6. Percent of explanation for the effects of climate, soil, and spatial processes on the Overall (a), Phytophage (b), and Predacity (c) fauna orders composition in East Asia.

Table captions:

Table 1. Summary of the soil animal community studies included in the dataset in East Asia.

Table 2. The sampling details for 14 sites in East Asia, Table 2. The sampling details for 14 sites in East Asia, where TH = Tahe, ARS = Aershan, CBS = Changbaishan, DLS = Donglingshan, BTM = Baotianman, BDGS = Badagongshan, TTS = Tiantongshan, SMT = Shimentai, JFL = Jianfengling, XSBN = Xishuangbanna, GH = Guanghua, SPK = Sapporo, HMA = Hiroshima, and YS = Yushan.

Table 3. Information on environment for 14 study sites in East Asia, where MAT = mean annual temperature, MTCM = mean temperature of the coldest months, EMT = extreme minimum temperature, MAP = mean annual precipitation, SOC = soil organic carbon, and SBD= soil bulk density

Table 4. Monte Carlo permutation tests results of environmental factors in East Asia. The "*", "**", and "***" represent p [?] 0.05, 0.01, and 0.001, respectively. (Note: MAT = mean annual temperature, MTCM = mean temperature of the coldest months, EMT = extreme minimum temperature, MAP = mean annual precipitation, SOC = soil organic carbon, and SBD = soil bulk density.)

Table 5. The rate of dissimilarity among species composition across all possible plot pairs along the spatial or environmental gradient in East Asia. The "*", "**", and "***" represent p [?] 0.05, 0.01, and 0.001, respectively. (Note: MAT = mean annual temperature, MTCM = mean temperature of the coldest months, EMT = extreme minimum temperature, MAP = mean annual precipitation, SOC = soil organic carbon, and SBD = soil bulk density.)

Table 1. Summary of the soil animal community studies included in the dataset in East Asia.

Study	Location	Vegetation	Soil type
Huang et al. (2008)	Tahe	*Larix olgensis, Populus davidiana,*and *Betula costata*	Brown coniferous forest soil
	52.33° N, 124.75° E		
Zhang et al. (2007)	Aershan	*Larix gmelini, Populus davidiana*	Brown coniferous forest soil
	47.18° N, 119.94° E		
Nakamura (1970)	Sapporo 42.87° N, 141.24° E	*Abies fabri*	Brown forest soil
Han (2015)	Changbaishan 43.65° N, 127.62° E	*Pinus koraiensis, Quercus mongolica, Acer mono,and Populus davidiana, Betula platyphylla*	Mountain dark brown soil
Xu etal. (2017)	Donglingshan 40.03° N, 115.47° E	*Quercus liaotungensis*	Brown soil
Kwon (2016)	Ganghwa	*Pinus densiflora*and *Quercus mongolica*	Mountain yellow soil
	37.61° N, 126.45° E		
Touyama (1994)	Hiroshima	*Pinus koraiensis, Piceaasper- ata,Tiliaamurensis*	Brown forest soil
	34.52° N, 132.23° E		
Xu (2020)	Baotianman 33.51° N, 111.94° E	*Quercus variabilis Blume, Quercus aliena var. acutidentata,* and *Pinus armandii.*	Mountain yellow brown soil
Yi (2005)	Tiantongshan	*Castanopsisfargesii, Schima superba,* and *Pinus massoniana*	Mountain yellow red soil
	29.80° N, 121.79° E		
He (2018)	Badagongshan 29.74° N, 110.06° E	*Fagus lucida, Liquidambar formosana,* and*Castanopsisfargesii*	Mountain yellow brown soil
Li et al. (2004)	Shimentai 24.45° N, 113.3° E	*Castanopsiseyrei, Schima superba, Pinus massoniana, Pinus elliottii,*	Mountainred soil
Chuan et al. (2003)	Yushan	*Tsuga chinen- sis,Yushanianiitakayamensis*soil	Mountain yellow red
	23.47° N, 120.89° E		
Yang et al. (1998)	Xishuangbannan 21.68° N, 101.45° E	*Hevea brasiliensis, Mallotuspaniculatus, Ppometia tomentosa, Terminalia myricocarpa*	Orthic acrisol

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Study	Location	Vegetation	Soil type
Xiong (2005)	Jianfengling 18.50° N, 109.00° E	*Antidesmamaclurei, Vaticamangachapoi, Lannea grandis, Aporosa chinensis*	Laterite and Yellow soil

Table 2. The sampling details for 14 sites in East Asia, Table 2. The sampling details for 14 sites in East Asia, where TH = Tahe, ARS = Aershan, CBS = Changbaishan, DLS = Donglingshan, BTM = Baotianman, BDGS = Badagongshan, TTS = Tiantongshan, SMT = Shimentai, JFL = Jianfengling, XSBN = Xishuangbanna, GH = Guanghua, SPK = Sapporo, HMA = Hiroshima, and YS = Yushan.

Site	Total number of individuals	Sampling area/m^2	Sampling volume/L	Sampling quantity	Sampling time /Month	Sampling layer/cm	Number of sampling locations	Number Repetit
TH	12841	0.84	126	336	6、8、10	Litter、0-5-10-15	7	4
ARS	9684	0.32	48	128	8、9	Litter、0-5-10-15	4	4
SPK	19012	0.88	44	440	1、5、7、9	0-5	11	10
CBS	24325	0.45	67.5	180	5、7、9	Litter、0-5-10-15	3	5
DLS	52673	1.81	270	480	4、6、8、10	Litter、0-5-10-15	10	4
GH	47919	0.39	39.25	400	9	0-5	20	10
HMA	18244	1.41	70.7	120	5、7、9	Litter、0-5	5	4
BTM	13063	0.31	47.1	640	5、9	Litter、0-5-10-15	16	5
TTS	13937	0.14	21.6	216	4、6、8、10	0-5-10-15	6	3
BDGS	12933	0.36	52.3	360	4、7、11	Litter、0-15	15	4
SMT	20045	2	100	400	9、10	Litter、0-5	20	5
YS	12860	0.42	32.4	324	4、6、8、10	0-5-10-15	3	3
XSBN	14434	0.16	23.55	180	7、8、9	0-5-10-15	4	5
JFL	37083	0.696	54	540	1、4、7、10	0-5-10-15	15	3

Table 3. Information on environment for 14 study sites in East Asia, where MAT = mean annual temperature, MTCM = mean temperature of the coldest months, EMT = extreme minimum temperature, MAP = mean annual precipitation, SOC = soil organic carbon, and SBD= soil bulk density

Sitename	Code	MAT ()	MTCM ()	EMT ()	MAP (mm)	SOC (g/kg)	SBD (kg/m^3)	pH	Reference
Tahe	TH	-2.4	-25.5	-32.6	428.0	2.8	11.1	5.5	Huang et al. (2008)

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Aershan	ARS	-3.2	-21	-31.5	441.4	2.2	11.8	6.5	Zhang et al. (2007)
Changbaishan	CBS	3.4	-15.6	-24.8	758.0	2.6	11.2	5.7	Han (2015)
DongLingshan	DLS	8	-7	-6.0	575.0	1.8	10.5	6.9	Xu et al. (2017)
Baotianman	BTM	15.1	1.5	-17.0	885.6	2	11.2	5.9	Xu (2020)
Badagongshan	BDGS	11.5	0.1	-0.2	2105.4	1.2	11.9	5.9	He (2018)
Tiantongshan	TTS	16.2	4.2	1.1	1374.7	1.4	12.7	5.8	Yi (2005)
Shimentai	SMT	20.8	10.9	4.5	2000.0	1.6	11.4	5.1	Li et al. (2004)
Jianfengling	JFL	24.5	19.4	16.4	2265.8	0.4	13.9	6.2	Xiong (2005)
Xishuangbanna	XSBN	21.8	10	5.00	1556.0	1	12	6	Yang et al. (1998)
Guanghwa	GH	10.3	-8.6	-8.6	1450.5	1.2	12.9	6	Kwon (2016)
Sapporo	SPK	8.5	-4	-14.1	738.0	5	9.2	5.1	Nakamura (1970)
Hiroshima	HMA	13.9	5	-2.0	1700.0	1.8	11.1	5.1	Touyama (1994)
Yushan	YS	9	4.3	-6.00	4000.0	1.6	11	4.4	Chuan et al. (2003)

Table 4. Monte Carlo permutation tests results of environmental factors in East Asia. The "*", "**", and "***" represent p [?] 0.05, 0.01, and 0.001, respectively. (Note: MAT = mean annual temperature, MTCM = mean temperature of the coldest months, EMT = extreme minimum temperature, MAP = mean annual precipitation, SOC = soil organic carbon, and SBD = soil bulk density.)

	Overall R^2	Overall Pr(>r)	Phytophage R^2	Phytophage Pr(>r)	Predacity R^2	Predacity Pr(>r)
Latitude	0.5227	**0.02***	0.6539	**0.004****	0.6086	**0.01****
MAT	0.4886	**0.028***	0.5362	**0.016***	0.5298	**0.019***
MTCM	0.4714	**0.035***	0.566	**0.012***	0.6468	**0.004****
EMT	0.3641	0.085	0.3293	0.098	0.5203	**0.01****
MAP	0.7765	**0.001*****	0.7527	**0.001*****	0.7322	**0.001*****
SOC	0.6292	**0.002****	0.5848	**0.001*****	0.3942	**0.04***
SBD	0.7279	**0.001*****	0.4508	**0.028***	0.2802	0.162
pH	0.0631	0.692	0.1238	0.5	0.2282	0.25

Table 5. The rate of dissimilarity among species composition across all possible plot pairs along the spatial or environmental gradient in East Asia. The "*", "**", and "***" represent p [?] 0.05, 0.01, and 0.001, respectively. (Note: MAT = mean annual temperature, MTCM = mean temperature of the coldest months, EMT = extreme minimum temperature, MAP = mean annual precipitation, SOC = soil organic carbon, and SBD = soil bulk density.)

	Overall	Overall	Overall	Overall	Phytophage	Phytophage	Phytophage	Phytophage	Predacity
	βj Slop	βj R^2	βs Slop	βs R^2	βj Slop	βj R^2	βs Slop	βs R^2	βj Slop
Latitude	0.025	**0.057***	0.019	**0.051***	0.035	**0.046***	0.036	**0.053***	0.054
MAT	0.003	0.033	0.002	0.031	0.008	**0.113****	0.008	**0.112****	0.008
EMT	0.002	**0.083****	0.002	**0.081****	0.006	**0.195*****	0.006	**0.199*****	0.005
MTCM	0.001	0.015	0.001	0.015	0.005	**0.112****	0.005	**0.113****	0.006
MAP	0.013	0.023	0.010	0.021	-0.004	0.000	-0.001	0.000	0.034
SOC	0.039	**0.176*****	0.033	**0.186*****	0.039	**0.07***	0.035	**0.062***	0.062
SBD	0.018	0.034	0.016	0.037	-0.015	0.009	-0.016	0.010	0.043

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