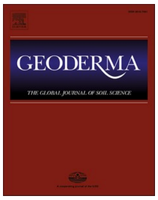
Geoderma 458 (2025) 117322

Contents lists available at ScienceDirect

Geoderma

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



Taxonomic and functional β-diversity of Collembola across elevational and seasonal gradients on a temperate mountain

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ARTICLE INFO

Handling Editor: Yvan Capowiez

Keywords:
Beta diversity
Conservation
Mountain
Season
Soil fauna

ABSTRACT

Understanding seasonal variations in community composition and species distribution along elevation gradients is a core task in biogeography and ecology but remains poorly studied, particularly in soil animal communities. In this study, we assessed seasonal β diversity of Collembola assemblages on Changbai Mountain, China. We sampled 18,942 individuals comprising 96 Collembola species across 10 altitudes (800 –2150 m) and measured five morphological traits (body length, number of ocelli, furca development, pigmentation and scales) of the species across three seasons. We then assessed both incidence-based and abundance-weighted taxonomic as well as functional β-diversity, and partitioned them into species turnover and nestedness, while also considering the contributions of particular species and elevation. Finally, we used multiple regression-based distance matrices to investigate the relative contribution of local habitat-related and climatic factors to β-diversity and their components. Overall taxonomic β-diversity, but not functional β-diversity, increased significantly with elevational distance. Generally, turnover components dominated taxonomic β-diversity across elevations, while both nestedness and turnover equally contributed to functional β-diversity. By contrast, both taxonomic and functional β-diversity varied inconsistently among seasons. The turnover components dominated taxonomic β-diversity across seasons, whereas the nestedness component contributed more to functional β-diversity. Furthermore, the local contribution to overall incidence-based taxonomic β-diversity followed a pronounced U-shaped pattern, indicates that lower and higher elevations significantly contribute to the biodiversity of Collembola communities. Notably, the local contribution to abundance-weighted taxonomic β-diversity decreased significantly with elevation in September but not in May and July. The species contributing to β-diversity varied not only between taxonomic and functional β-diversity but also between seasons. Temperature strongly influenced both taxonomic and functional β-diversity patterns, underscoring its role in shaping Collembola diversity across elevation. Soil pH correlated with functional β-diversity and its turnover component in September but not in May and July. Our findings highlight the importance of incorporating seasonal variations in biodiversity assessments and underscore the contribution of lower and higher elevations to biodiversity conservation in mountainous regions.

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https://doi.org/10.1016/j.geoderma.2025.117322
Received 10 January 2025; Received in revised form 22 April 2025; Accepted 27 April 2025

1. Introduction

Mountains are hotspots of biodiversity covering steep environmental gradients within short geographic distances (Körner, 2007; Sanders and Rahbek, 2012). With ongoing global changes in climate and land use, the role of mountains as refugia for biodiversity may be increasingly threatened (Rahbek et al., 2019). Compared to above-ground biota, the elevational and seasonal patterns of below-ground communities remain underexplored. Soil animals play crucial roles in preventing erosion, stabilizing slopes, enhancing soil structure and fertility, and supporting biodiversity (Bardgett and van der Putten, 2014; Nielsen, 2019), which are essential functions in mountain regions. Therefore, it is critical to understand the processes structuring soil animal communities, and to implement conservation strategies targeting soil animal diversity in mountain regions.

β-diversity describes the variation in species composition among sites in response to environmental changes (Bishop et al., 2015; Kraft et al., 2011), and is increasingly considered by conservation scientists for identifying conservation strategies (Angeler, 2013; Socolar et al., 2016). It comprises two components: (1) turnover, which is the variation in species composition due to the replacement of species, and (2) nestedness, which quantifies to what extent the species composition of one community is a subset of another, typically resulting from species loss rather than replacement (Baselga, 2010; Legendre, 2014). Understanding the relative contributions of the two components allows deeper insight into the processes structuring communities, with high turnover indicating species replacement driven by environmental filtering (Nunes et al., 2016; Wu et al., 2023), while the dominance of nestedness reflecting historical constraints or dispersal limitation (Qian et al., 2005). Climatic (e.g., precipitation and temperature) and local habitat-related factors (e.g., soil carbon and nitrogen content) are shaping β-diversity along elevational gradients (Lin et al., 2023; Wang et al., 2019). Additionally, β-diversity is influenced by seasonal fluctuations and this needs to be considered in conservation strategies (Bishop et al., 2015). Integrating turnover and nestedness into conservation strategies allows to prioritize conservation efforts, with turnover suggesting the need to protect multiple sites and nestedness indicating to focus on species-rich sites (Angeler, 2013; Socolar et al., 2016).

To further refine conservation strategies, partitioning β-diversity into local contributions (LCBD) and species contributions (SCBD) helps identify unique sites and species for prioritized conservation (Legendre and De Cáceres 2013, Dirilgen et al. 2018, Wang et al. 2019, Zhao et al. 2021). LCBD represents the degree to which a site contributes uniquely to regional β-diversity, whereas SCBD indicates the relative contribution of a species to overall community dissimilarity. As a result, sites and species with higher LCBD and SCBD values should be prioritized for conservation efforts (Legendre and De Cáceres, 2013; Hill et al., 2021). Additionally, taxonomic β-diversity can be measured using incidence-based or abundance-weighted metrics, which emphasize rare and dominant species, respectively, providing complementary insights into spatial community structure (Anderson, 2006; Anderson et al., 2011; Baselga, 2013).

Taxonomic metrics alone may not reveal the ecological processes shaping variations in community composition along elevation gradients. A functional trait is a measurable characteristic that influences the organism's fitness, its effect on other organisms and on the environmental (Joimel et al., 2024; Pey et al., 2014). Considering functional traits adds to taxonomic metrics by allowing to assess shifts in ecological strategies along environmental gradients. While many studies on the functional diversity of soil invertebrates rely on mean species trait values from literature or databases, direct field-based trait measurements remain relatively rare. In this study, we provide trait values measured directly from Collembola specimens collected in the study area, enhancing the ecological relevance of our functional analyses. Functional β-diversity, which captures variation in community composition based on species traits rather than taxonomic identity, provides additional insight into the ecological processes shaping biodiversity patterns along environmental gradients (Laliberte et al., 2010; Swenson, 2011). Previous studies used functional β-diversity to explore trait-based community assembly mechanisms (Ricotta et al., 2020; Zhao et al., 2021), but its application to soil fauna along elevation gradients remains limited. Collembola, one of the most abundant and diverse soil microarthropods, contribute to essential ecosystem processes such as carbon and nitrogen cycling, soil microstructure formation, and plant litter decomposition (Deharveng, 2004; Hopkin, 1997). These functions are linked to Collembola traits which vary with environmental conditions. For example, body length is closely linked to physiological attributes of species (e.g., metabolic rates) and reflects microhabitat characteristics the species live in (Ellers et al., 2018; Moretti et al., 2017). Previous studies proved the body length of Collembola to not only vary with environmental or elevational gradients but also with season (Xie et al., 2024; Yoshida and Hijii, 2014). Other traits correlating with elevation and season include number of ocelli, furca length, pigmentation and scales, with each of them potentially helping species to cope with environmental stressors (Susanti et al. 2021, Xie et al. 2022b). While previous studies examined Collembola community composition along elevation gradients (Bokhorst et al., 2018; García-Gómez et al., 2009; Xie et al., 2022b), no study has simultaneously assessed β-diversity across taxonomic and functional dimensions, and incorporated seasonal variations.

In this study, we applied multi-component, i.e. taxonomic (both incidence-based and abundance-weighted) and functional diversity, and multi-partitioning approaches of β-diversity to assess the distribution of Collembola assemblages along an elevation gradient on Changbai Mountain, northeast China. Specifically, we examined (1) the patterns of taxonomic and functional β-diversity of Collembola communities along the studied elevational gradient, (2) seasonal variations in taxonomic and functional β-diversity of Collembola communities along the elevations, and (3) local habitat-related and climatic factors shaping Collembola diversity patterns and community assembly. Overall, we aimed at evaluating the power of β-diversity partitioning to inform about conservation strategies for soil invertebrates.

2. Material and methods

2.1. Study area

The study was carried out along the north slope of the Changbai Mountain Nature Reserve (hereafter referred to as Changbai Mountain) in northeast China (41°41′–42°51′N; 127°43′–128°16′E, Fig. 1). Established in 1960, the reserve is one of the few protected close-to-natural mature temperate forests in Asia (Stone, 2006; Xue and Tisdell, 2001). The region falls within the temperate zone and experiences a typical temperate continental monsoon climate characterized by dry, windy springs, short rainy summers, and cool autumns with a high frequency of fog and prolonged cold winters. This pronounced seasonality significantly influences the local ecosystems and the dynamics of species inhabiting the area. Changbai Mountain can be divided into five distinct vertical vegetation zones: (1) a mixed coniferous and broad-leaved forest zone below 1100 m, (2) a mixed coniferous forest zone between 1100 and 1500 m, (3) a sub-alpine mixed coniferous forest zone between 1500 and 1800 m, (4) a birch forest zone between 1800 and 2100 m, and (5) an alpine tundra zone above 2100 m (Bai et al. 2011; Zou et al. 2014).

2.2. Field sampling, species identification and species traits

In May, July, and September 2015, we sampled litter and soil from ten different elevations (800, 950, 1100, 1250, 1400, 1550, 1700, 1850, 2000 and 2150 m) along the northern slope of Changbai Mountain. More detailed maps of the sampling sites are provided in Ji et al. (2024) and Xie et al. (2022a, b). May represents late spring, with temperatures ranging from 5 °C to 15 °C, moderate rainfall and active vegetation

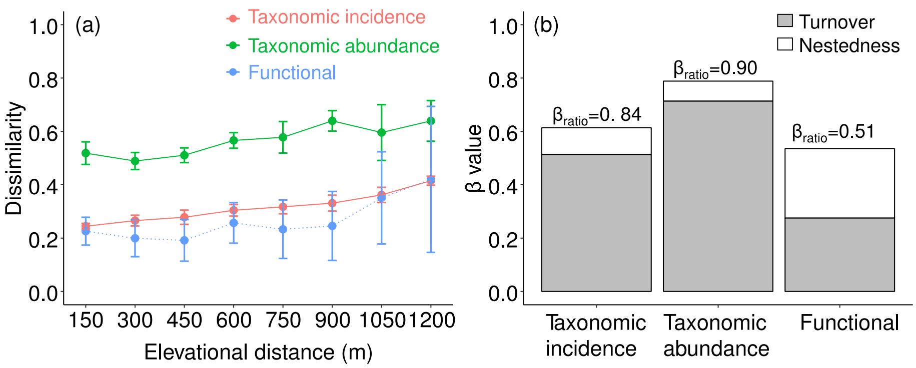

Fig. 1. Taxonomic (incidence-based and abundance-weighted) and functional pairwise β-diversity of Collembola communities along an elevational gradient on Changbai Mountain and the relative contributions of spatial turnover and nestedness components. (a) Taxonomic (incidence-based and abundance weighted) and functional pairwise β-diversity of Collembola communities along an elevational gradient; solid lines represent significant relationships based on (partial) Mantel tests (Table 2), while dotted lines indicate non-significant trends. (b) Relative contributions of spatial turnover and nestedness components to total taxonomic (both incidence-based and abundance-weighted) and functional β-diversity; the β_{ratio} represents the ratio between the turnover component and total β-diversity.

growth after snowmelt. July corresponds to mid-summer, is warm and humid (15 °C–25 °C) with the highest annual precipitation. By September early autumn sets in, bringing cooler temperatures (5 °C–15 °C), reduced rainfall and a gradual decline in plant growth (Wang et al., 2020; Yu et al., 2011). At each elevation, we established five randomly selected plots measuring 10 m^2, spaced at least 100 m. From each plot, three random subsamples of litter and soil were taken and combined to form a single litter and soil sample, respectively.

Litter samples were with a 100 cm^2 frame, while soil samples were taken using a 5.5 cm diameter core to a depth of 10 cm beneath the litter layer. Soil animals in litter and soil were extracted using Berlese funnels with a diameter of 20 cm, equipped with mesh sizes of 2 mm for litter and 0.84 mm for soil. Extraction was conducted over a period of ten days without heating. Extracted soil fauna were preserved in 95 % ethanol for subsequent identification. Extraction procedures started as soon as possible after sample collection, with a maximum delay of 24 h.

Collembola specimens were separated from other soil-dwelling organisms and sorted into distinct morphological species using a stereomicroscope (STEMI 508, Zeiss, Jena, Germany) based on discernible morphological traits. To ensure accuracy, a minimum of eight individuals representing each morphological species from every sample were subsequently subjected to cleaning with lactic acid, mounted in Hoyer's solution and examined using a Zeiss Axio Scope A1 microscope. Collembola were identified to species or morphospecies using pertinent literature sources (Christiansen & Bellinger, 1998; Potapov, 2001; Sun et al. 2020; Xie et al. 2019). Immature specimens were sorted to species / morphospecies by comparison with adults or subadults found within the same sample or in additional samples from the same locality.

We selected five morphological traits associated with diet and habitat preferences of Collembola: body length, number of ocelli, furca development, pigmentation and scales. Body length was measured for individual specimens as a line following the natural curvature of the body, from the head to the end of the abdomen, excluding appendages (ten randomly chosen adult individuals per species per sample, if possible) using a Nikon SMZ800 microscope and Nikon DS-Fi1 camera. Each species was assessed for the number of ocelli (ranging from zero to eight), furca development (absent, short, long), pigmentation (absent, diffuse, patterned), and presence or absence of scales. Previous studies have linked these morphological traits in Collembola to their potential functions as effect traits (Bonfanti et al., 2024) and their response to environmental conditions as response traits (Qiao et al., 2022; Santorufo et al., 2014; Yu et al., 2022), and we also classified the studied Collembola traits into these two categories (**Table S1**). For instance, pigmentation is often linked to UV radiation tolerance, while furca development determines species' ability to evade predation in exposed habitats. The complete list of species and their corresponding trait values is provided in **Table S2**.

2.3. *Environmental variables*

To evaluate potential drivers of taxonomic and functional β-diversity along the elevation gradient, we used local environmental factors and current climate conditions i.e., air and soil temperature. Precipitation and temperature correlated closely. The selected environmental factors included total nitrogen (N) and total carbon (C) concentrations (determined using an elemental analyzer; vario MACRO cube, Elementar), soil moisture (gravimetrically) and pH (1:5 wt/vol soil–water suspension), and carbon-to-nitrogen ratio (C/N ratio) in both litter and soil across all three seasons. Three climatic variables were extracted: soil annual mean temperature and temperature seasonality from 0–5 cm soil depth extracted from SoilTemp (Lembrechts et al. 2021), and annual mean air temperature extracted from WorldClim (Fick and Hijmans, 2017). These climatic data were obtained for the mean coordinates of the sampling plots at the ten different elevations using the R package 'raster' (Robert, 2021).

2.4. *Statistical analysis*

Species accumulation curves and rarefaction curves were used to inspect sampling effort and completeness across different seasons using the *specaccum* function in the 'vegan' package (Oksanen et al. 2019) and the *iNEXT* function in the 'iNEXT' package (Hsieh et al. 2016). The community data from each sampling plot in May, July and September were aggregated to represent the overall diversity at each elevation. All analyses were performed using R software version 4.1.2 (R Core Team, 2022).

2.4.1. *β-diversity partitioning: turnover and nestedness components.*

To assess variations in overall taxonomic and functional β-diversity along the elevation gradient, we employed the partitioning approaches proposed by Baselga (2010, 2012). Additionally, we analyzed the β-diversity index for each elevational site (800, 950, 1100, 1250, 1400, 1550, 1700, 1850, 2000 and 2150 m). Pairwise and multiple-site dissimilarity partitioning were calculated using functions in the 'betapart' package (Baselga et al., 2022). Mantel tests with Spearman's method were used to examine the correlation between β-diversity (and its components) and elevation across all seasons. All β-diversity abbreviations and their explanation are provided in Table 1.

Following this approach, the incidence-based pair-wise β-diversity, measured as Sørensen dissimilarity (βsor) was further partitioned into two additive components: (1) spatial turnover (excluding the effect of species richness variation), derived by applying the Simpson

Table 1
List of abbreviations and explanations of β-diversity metrics used in this study.

Abbreviation	Data frame	Explanation
βsor	Incidence-based pair-wise	Sørensen pair-wise dissimilarity
βsim	Incidence-based pair-wise	spatial turnover (replacement), measured as Simpson dissimilarity index
βsne	Incidence-based pair-wise	the nestedness-fraction of Sørensen pair-wise dissimilarity
βbray	Abundance-based pair-wise	total abundance-based dissimilarity between sites, measured as the Bray-Curtis index
βbray.bal	Abundance-based pair-wise	balanced variation in abundance between sites
βbray.gra	Abundance-based pair-wise	where individuals are lost from one site to another
funct.βsor	Pair-wise functional	functional beta diversity, Sørensen-derived pairwise functional dissimilarity
funct.βsim	Pair-wise functional	functional turnover, measured as Simpson derived pairwise functional dissimilarity
funct.βsne	Pair-wise functional	nestedness fraction of the Sørensen-derived pairwise functional dissimilarity
βSOR	multiple-site	overall beta diversity, incidence-based multiple-site dissimilarities
βSIM	multiple-site	turnover component, measured as Simpson dissimilarity
βSNE	multiple-site	nestedness-resultant fraction of Sørensen dissimilarity
βBRAY	Abundance-based multiple-site	overall dissimilarity, measured as Bray-Curtis multiple-site dissimilarity
βBRAY.BAL	Abundance-based multiple-site	balanced variation component of Bray-Curtis multiple-site dissimilarity
βBRAY.GRA	Abundance-based multiple-site	abundance-gradient component of Bray-Curtis multiple-site dissimilarity
FUNCT.β SOR	Multiple-site functional	overall functional beta diversity, measured as Sørensen derived functional dissimilarity
FUNCT.βSIM	Multiple-site functional	functional turnover, measured as Simpson derived functional dissimilarity
FUNCT.βSNE	Multiple-site functional	nestedness-resultant fraction of Sørensen derived functional dissimilarity

dissimilarity index (βsim), and (2) nestedness (βsne), calculated as the difference between βsor and βsim. The *beta.pair* function was used for incidence data.

Abundance-weighted pair-wise β-diversity (βbray) was further divided into two components: (1) balanced variation in abundance (βbray.bal), where individuals of some species at one site are replaced by an equal number of individuals from different species at another site, and (2) abundance gradients (βbray.gra), where individuals are lost from one site to another. This partitioning follows the method proposed by Baselga (2013) for the Bray–Curtis dissimilarity index. The abundance framework parallels the partitioning of β-diversity into spatial turnover and nestedness components, with βbray.bal representing abundance turnover and βbray.gra representing abundance nestedness (Loiseau et al. 2017). The *beta.pair.abund* functions was used for abundance-weighted data.

Pairwise functional β-diversity (funct.βsor) was calculated as Sørensen-derived pairwise functional dissimilarity and divided into two components (Villéger et al. 2011, 2013; Baselga 2012): (1) functional turnover (funct.βsim), derived from the Simpson pairwise functional dissimilarity, and (2) nestedness-resultant functional dissimilarity (funct.βsne), representing the nestedness fraction of the Sørensen-derived pairwise functional dissimilarity. To calculate pairwise functional β-diversity, we first computed functional dissimilarity between all species pairs using Gower's distance, which accommodates both categorical and continuous traits in our data (Gower, 1971). Next, principal coordinate analysis (PCoA) was performed on the functional distance matrix (Laliberté & Legendre, 2010; Villéger et al., 2008), with the first three axes used to define a multidimensional functional space. Pairwise functional β-diversity was calculated using the *functional.beta.pair* function.

To assess the relative importance of turnover and nestedness components in overall β-diversity, we used multiple-site partitioning approaches as proposed by Baselga (2010, 2012). Multiple-site dissimilarity values were denoted by capital letters to differentiate from pairwise β-diversity, which was also calculated using functions in the 'betapart' package. Specifically, incidence-based multiple-site dissimilarities (βSOR) were calculated using the *beta.multi* function, abundance-based multiple-site dissimilarities (βBRAY.BAL) were calculated using the *beta.multi.abund* function, and multiple-site functional dissimilarities (FUNCT.βSOR) were calculated using the *functional.beta.multi* function. The ratio between the turnover component and the overall multiple-site dissimilarity indicates the relative contribution of the turnover component to Collembola assemblages along the elevation gradient.

2.4.2. *β-diversity partitioning: Species and local contributions*

To comprehend the contribution of particular species and elevation to components of β-diversity, we used the partitioning method proposed by Legendre and De Caceres (2013) and Nakamura et al. (2020). The partitioning of taxonomic (both incidence-based and abundance-weighted) β-diversity was calculated using the *beta.div* function in the 'adespatial' package (Legendre and De Cáceres 2013). First, we computed the total variation of the community matrix as β-diversity (hereafter referred to as BD for results based on incidence-based community data, and A-BD for results based on abundance-weighted community data). Subsequently, BD was partitioned into the contribution of species (SCBD; reflecting the degree of variation of individual species across elevations) and local contribution (LCBD; serving as indicator of the ecological uniqueness of individual elevations). Similarly, we denoted results based on abundance-weighted community data as A-SCBD and A-LCBD, respectively.

Additionally, we partitioned functional β-diversity following Nakamura et al. (2020), who expanded the BD framework to derive functional dimensions of diversity (BDfun). Consequently, BDfun was partitioned into species (XSCBD for BDfun) and local (XLCBD for BDfun) contributions. The code is available on Zenodo at https://doi.org/10.5281/zenodo.3817980 (Nakamura et al. 2020). Furthermore, to investigate the relationships between local contribution and elevation gradient, we employed linear and quadratic models, selecting the model with better goodness of fit based on lower value of the Akaike information criterion (AIC) (Yamaoka, Nakagawa & Uno, 1978).

2.4.3. *Predictors of β-diversity.*

To assess the relative contribution of environmental and climatic factors to β-diversity along elevation gradients, we employed a multiple regression on distance matrices (MRM) approach combined with variance partitioning (Lichstein 2007; Swenson, 2014). This method is conceptually similar to traditional multiple regression, but with all variables being distance matrices instead of raw data and significance being calculated through permutation tests (10,000 runs). Doing this, we modeled full triangular β dissimilarity matrices (i.e., βsor, βsim and βnes), encompassing all pairwise comparisons between elevational sites, against corresponding environmental and climatic distance matrices (i.e., soil pH distance, C/N ratio distance, mean soil temperature distance, seasonal soil temperature distance and seasonal air temperature distance). Standardized partial regression coefficients (β) were then estimated to assess the relative importance of each predictor variable on β-diversity patterns. Finally, the *lm* function was used to determine the proportion of variance explained (R^2) by each model (Swenson, 2014). MRM analysis was conducted using the *MRM* function in the 'ecodist' package (Goslee and Urban, 2007).

3. Results

A total of 96 Collembola species / morphospecies of 12 families and 47 genera were identified from a total of 18,942 individuals, including 79 species from 5,717 individuals collected in May, 84 species from 7,834 individuals collected in July and 49 species from 5,391 individuals collected in September. Collembola communities at all altitudes were sampled sufficiently in May, July and September as indicated by marginally asymptotic species accumulation curves and stabilizing rarefaction curves (**Figs. S1, S2**).

3.1. Turnover and nestedness components in taxonomic and functional β-diversity

Taxonomic (both incidence-based and abundance-weighted) and functional β-diversity of Collembola communities ranged from 0.25 to 0.75, across elevations and seasons (**Fig. S3**). For taxonomic β-diversity the turnover component generally contributed most, while for functional β-diversity it was the nestedness component (except at 800 m). Total taxonomic (incidence-based and abundance-weighted) β-diversity increased significantly with elevation distance but not total functional β-diversity (Fig. 1**a,** Table 2). The turnover (βsim and βbray.bal) but not the nestedness components (βsne and βbray.gra) of taxonomic (incidence-based and abundance-weighted) and functional diversity significantly increased with elevation distance. Generally, across elevations the turnover components (βSIM and βBAL) predominated the incidence-based and abundance-weighted taxonomic multiple-site β-diversity (Fig. 1**b**). By contrast, nestedness and turnover components contributed equally to the functional β-diversity across elevations.

In contrast to the pattern across seasons, both taxonomic (incidence-based and abundance-weighted) and functional β-diversity varied inconsistently between seasons. In May, both incidence-based taxonomic and functional β-diversity as well as their respective components (turnover and nestedness) significantly increased with elevation distances, but this was not the case in abundance-weighted taxonomic β-diversity (**Fig. S4a-c,** Table 2). In July, taxonomic (incidence-based and abundance-weighted) β-diversity and turnover components increased significantly with elevation distances, but this was not the case for the nestedness component. In September, β-diversity and its components displayed inconsistent patterns. Similar to the pattern across seasons, the turnover components (βSIM and βBAL) of β-diversity dominated taxonomic (incidence-based and abundance-weighted) β-diversity in each season, whereas the nestedness component contributed most to functional β-diversity (**Fig. S4d-e**). Seasonal variations in taxonomic and functional β-diversity were inconsistent, possibly reflecting species-specific responses to seasonal environmental changes such as temperature fluctuations and resource availability.

3.2. Species and local contributions to taxonomic and functional β-diversity

The local contribution to incidence-based taxonomic β-diversity across seasons followed a pronounced U-shaped pattern, while the relationships in abundance-weighted taxonomic and functional β-diversity did not change significantly with elevation (Fig. 2**a-c**). Total variations in incidence-based taxonomic, abundance-weighted taxonomic and functional β-diversity of Collembola communities were 0.298, 0.292 and 0.002, respectively. Local communities contributed 7.8—16.1 % to total variation in incidence-based taxonomic β-diversity, 6.2—17.3 % to abundance-weighted taxonomic β-diversity and 1.6—27.8 % to functional β-diversity (**Table S3**). In contrast to the pattern across seasons, the local contribution to abundance-weighted taxonomic β-diversity significantly increased with elevation in September (**Fig. S5**).

Across seasons the most important species contributing to taxonomic and functional β-diversity varied (Fig. 3d-f, S6). For incidence-based taxonomic β-diversity, a wide range of species were of similar importance, but the key species belonged to the genus *Superodontella* in May, July and September. Whereas *Tetracanthella wui* stood out as key species for abundance-weighted taxonomic β-diversity across seasons, characterized by its widespread distribution and high abundance. For functional β-diversity, the genera *Pogonognathellus* and *Tomocerus* were most important, both among the largest Collembola species with distinct morphological traits in our study, though the specific contributors varied across seasonally.

3.3. Factors explaining β-diversity patterns

For taxonomic β-diversity, the full models of environmental distances explained 81.2 % of the total variation across seasons and 66.2 % in May, 52.3 % in July and 25.9 % in September (Tables 3, 4). For incidence-based taxonomic β-diversity, both the across season turnover component and the total β-diversity in July showed a significant positive correlation with soil C/N ratio distances (Fig. 3, S7). Furthermore, in May total incidence-based taxonomic β-diversity and both of its components, the total β-diversity and its nestedness component, increased with mean soil temperature difference. By contrast, soil seasonal temperature only correlated with the nestedness component of β-diversity, with no significant relationship in May, July and September. Air seasonal temperature correlated with total β-diversity as well as its turnover component across seasons and in May. Soil pH generally did not correlate with incidence-based taxonomic β-diversity or its components across seasons and in July and September, except for the turnover component in September.

For abundance-weighted β-diversity, the full models of environmental distances accounted for 37.0 % of the total variation across seasons and 45.3 % in May, 29.9 % in July and 26.1 % in September. Notably, total abundance-weighted β-diversity and its turnover component across seasons and in May significantly increased with soil C/N ratio distances, whereas its nestedness component significantly decreased with soil C/N ratio distances (**Fig. S8**). Additionally, air seasonal temperature distance positively correlated with overall abundance-weighted β-diversity across seasons and in May (Table 4). Neither mean soil temperature distance nor soil seasonal temperature distance correlated with abundance-weighted taxonomic β-diversity across seasons and in the three seasons, and the same was true for soil pH.

Regarding functional β-diversity, the full models of environmental distances accounted for 64.5 % (βsor) of the total variation across

Table 2
Relationship between β-diversity (incidence-based and abundance-weighted taxonomic β-diversity, as well as functional pairwise β-diversity) and elevation on Changbai Mountain. The analysis includes overall β-diversity (βsor and βbray) and its spatial turnover (βsim and βbray.bal) and nestedness (βsne and βbray.gra) components. *p < 0.05, **p < 0.01, ***p < 0.001.

	Dissimilarity index	Total	May	July	September
Taxonomic incidence	βsor	**0.684*****	**0.786*****	**0.556*****	0.194
	βsim	**0.541*****	**0.314***	**0.417*****	0.204
	βsne	0.217	**0.461***	0.023	−0.054
Taxonomic abundance	βbray	**0.363***	0.235	**0.437****	0.182
	βbray.bal	**0.273***	0.160	**0.409****	0.218
	βbray.gra	−0.015	0.096	−0.033	−0.023
Functional	βsor	0.299	**0.655****	0.017	−0.002
	βsim	**0.373***	**0.416***	−0.011	0.094
	βsne	0.185	**0.459***	0.022	−0.074

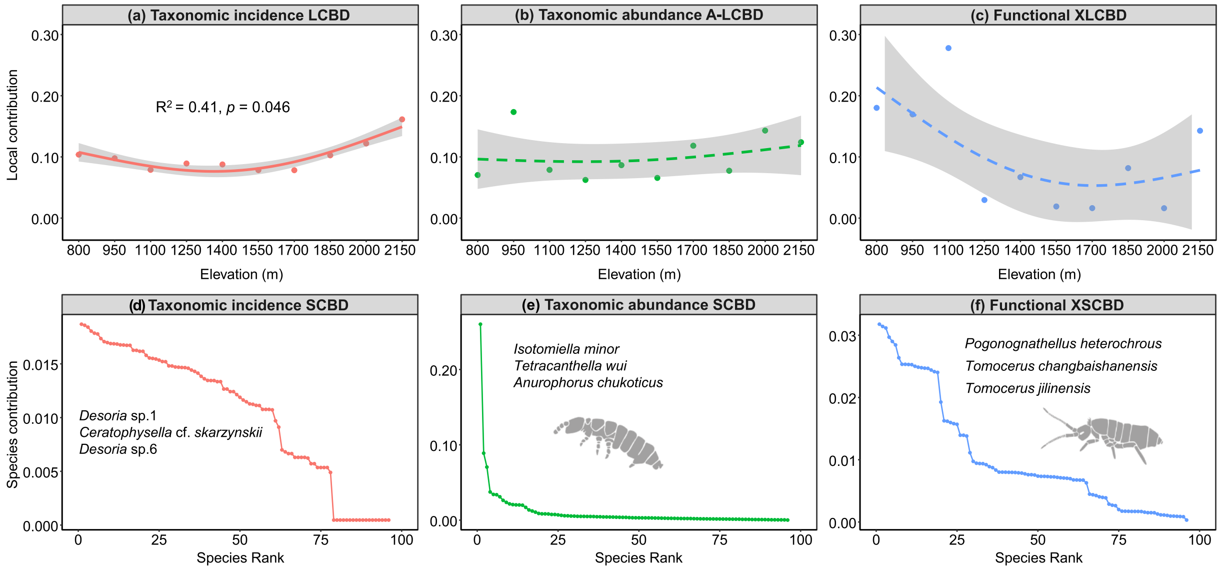

Fig. 2. Local and species contributions to taxonomic (incidence-based and abundance-weighted) and functional pairwise β-diversity. (a-c) Local contributions of elevation plots to incidence-based taxonomic, abundance-weighted taxonomic and functional pairwise β-diversity; as well as (d-f) contributions of Collembola species to incidence-based taxonomic, abundance-weighted taxonomic and functional pairwise β-diversity on Changbai Mountain, species ranked by their relative contribution. Each dot represents a species; the names represent the three most important species.

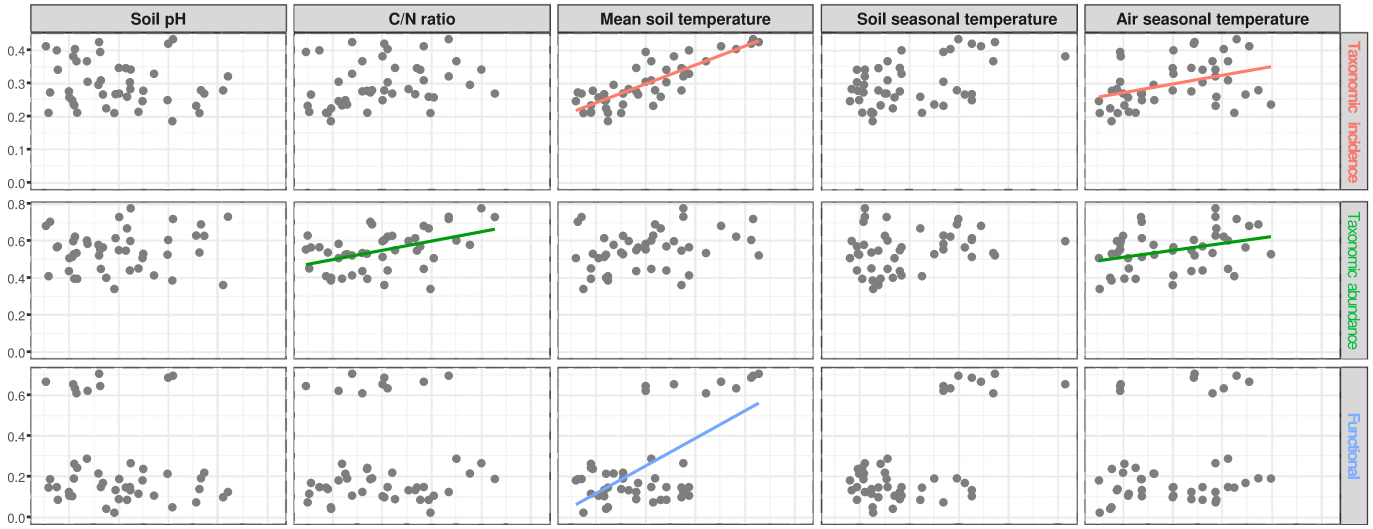

Fig. 3. Regressions between distances of environmental variables (soil pH, C/N ratio, mean soil temperature, soil seasonal temperature and air seasonal temperature) and incidence-based taxonomic, abundance-weighted taxonomic and functional pairwise β-diversity; Only significant regression lines are plotted, $p < 0.05$.

Table 3

Multiple regressions between distances of environmental variables (soil pH, C/N ratio, mean soil temperature, soil seasonal temperature and air seasonal temperature) and taxonomic (both incidence-based and abundance-weighted) as well as functional pairwise β-diversity (βsor and βbray) and its spatial turnover (βsim and βbray.bal) and nestedness (βsne and βbray.gra) components. In each model, the variation explained by the full model (R^2) and the slope of the regression line for each single predictor are given. Significant effects are emphasized in bold.

Characteristics	Taxonomic incidence			Taxonomic abundance			Functional		
	βsor	βsim	βsne	βbray	βbal	βgra	βsor	βsim	βsne
pH	−0.011	−0.009	−0.002	0.013	0.018	−0.006	−0.042	−0.003	−0.039
C/N	0.018	**0.022***	−0.003	**0.05****	**0.075****	**−0.025***	0	0.015	−0.015
soiltemp_mean	**0.057*****	**0.035****	**0.022***	0.035	0.024	0.012	**0.135***	**0.048***	0.088
soiltemp_season	0.032	0.008	**0.024***	0.026	0.001	0.024	0.138	0.043	0.095
airtemp_season	**0.026***	**0.025***	0.001	**0.037***	0.029	0.009	0.036	0.023	0.014
Full Model R^2	**0.812*****	**0.4266****	0.3305	**0.3695***	0.2886	0.1491	0.6448	0.3498	0.5968

Table 4
Multiple regressions between distances of environmental variables and taxonomic (both incidence-based and abundance-weighted) as well as functional pairwise β-diversity (βsor and βbray) and its spatial turnover (βsim and βbal) and nestedness (βsne and βgra) components in May, July and September. In each model, the variation explained by the full model (R^2) and the slope of the regression line for each single predictor are given. Significant effects are emphasized in bold.

May	Taxonomic incidence			Taxonomic abundance			Functional		
Characteristics	βsor	βsim	βsne	βbray	βbal	βgra	βsor	βsim	βsne
pH	0.007	0.051	0.075	0.012	0.001	0.029	0.005	0.072	0.005
C/N	0.091	0.010	0.038	__0.246__**	__0.147__*	−0.018	0.055	0.067	0.011
soiltemp_mean	__0.592__***	0.092	__0.207__*	0.043	0.007	0.028	__0.262__**	__0.198__*	__0.085__*
soiltemp_season	0.101	0.014	0.158	0.030	0.018	0.002	0.002	0.001	0.002
airtemp_season	__0.219__**	__0.190__**	0.003	__0.234__**	__0.094__*	0.052	__0.226__**	__0.402__**	0.022
Full Model R^2	__0.6620__***	__0.3261__*	__0.4458__*	__0.4532__*	__0.2732__*	0.0978	__0.4475__*	__0.5470__**	0.1704
July	Taxonomic incidence			Taxonomic abundance			Functional		
Characteristics	βsor	βsim	βsne	βbray	βbal	βgra	βsor	βsim	βsne
pH	0.018	0.025	0.002	0.093	0.029	0.007	0.005	0.035	0.001
C/N	__0.163__*	0.007	0.051	0.056	__0.096__*	0.009	0.024	0.001	0.026
soiltemp_mean	__0.308__**	__0.161__*	0.001	0.125	__0.145__*	0.005	0.018	0.033	0.005
soiltemp_season	0.075	0.023	0.004	0.011	0.028	0.005	0.054	__0.329__**	0.001
airtemp_season	0.011	0.050	0.018	0.001	__0.132__*	__0.110__*	0.005	0.032	0.001
Full Model R^2	__0.5232__**	0.1758	0.1178	0.2993	0.2639	0.1365	0.092	__0.3607__*	0.0322
September	Taxonomic incidence			Taxonomic abundance			Functional		
Characteristics	βsor	βsim	βsne	βbray	βbal	βgra	βsor	βsim	βsne
pH	0.042	__0.147__*	0.056	0.013	0.001	0.011	__0.128__*	__0.373__**	0.025
C/N	0.007	0.147	0.084	0.055	0.031	__0.100__*	0.009	0.044	0.006
soiltemp_mean	0.021	0.045	0.011	0.008	__0.154__*	0.052	0.002	0.021	0.023
soiltemp_season	0.113	0.001	0.092	0.136	0.085	0.004	0.012	0.016	0.037
airtemp_season	0.039	0.004	0.056	0.003	0.017	0.003	0.001	0.007	0.008
Full Model R^2	0.2591	0.2654	0.4514	0.2611	0.2208	0.2753	0.2308	__0.4551__*	0.1907

seasons and 44.8 % in May, 9.2 % in July and 23.1 % in September (Table 4). Among the environmental variables considered, soil pH only positively correlated with functional β-diversity and its turnover component in September. Total functional β-diversity and its turnover component in the across season and in May significantly increased with mean soil temperature distance (**Fig. S9**). Total functional β-diversity and its turnover component in May significantly increased with seasonal air temperature distance.

4. Discussion

We assessed elevational and seasonal changes in taxonomic and functional β-diversity of Collembola communities using two partitioning frameworks (species turnover and nestedness components as well as species and local site contributions) based on incidence-based and abundance-weighted community data on Changbai Mountain. Generally, turnover was the dominant component of taxonomic β-diversity (both incidence-based and abundance-weighted). By contrast, functional β-diversity was shaped by both turnover and nestedness across elevations, with nestedness being more prominent in May, July and September. Furthermore, total taxonomic (incidence-based and abundance-weighted) β-diversity increased significantly with elevation distance but not functional β-diversity. Specifically, taxonomic β-diversity significantly increased with elevation distance in May and July, but not in September, and functional β-diversity showed this pattern only in May. Partitioning of β-diversity into contributions of species and elevations revealed that lower and higher elevations tended to contribute more to β-diversity than intermediate elevations, but these contributions varied with season, with higher elevations only contributing more to abundance-based β-diversity in September. Further, the contribution of specific species differed between seasons, but this varied between taxonomic and functional approaches. Notably, taxonomic β-diversity was strongly associated with soil C/N ratio suggesting that variations in soil resource quality influence species replacement across elevations. While this was not the case in functional β-diversity, the C/N ratio likely influences Collembola diversity through changes in nutrient availability during litter decomposition. Moreover, temperature was the main factor explaining both incidence-based taxonomic and functional β-diversity across the elevation gradient, highlighting the prominent role of temperature-driven mechanisms for the origin and maintenance of biodiversity of Collembola.

4.1. *Turnover and nestedness components in taxonomic (incidence-based and abundance-weighted) and functional β-diversity*

Generally, for changes in community composition of Collembola across elevations species turnover was more important than nestedness, and this was similar for abundance-weighted indices. This pattern is consistent with previous findings on canopy Collembola (Wu et al., 2023), soil oribatid mites (Liu et al., 2023) and enchytraeids (Jiang et al., 2019) from the same study area. A number of Collembola species only occurred at few elevations and nine species only occurred at a single elevation (“endemic” species, **Fig. S10**). The pattern may be driven by sampling effect, as studies have shown that short-term assessments tend to emphasize the taxonomic turnover component due to missing detection of species whereas long-term studies are likely to emphasize the nestedness component (Dapporto et al., 2014). However, in our study the sampling effect was in fact likely weak because each elevation was sampled across seasons, i.e. in May, July and September. The high turnover of species among elevations therefore points to deterministic processes driven by environmental filtering (Ding et al., 2024) due to changes in temperature, soil moisture and litter depth from the foot to the summit of Changbai Mountain.

In contrast to the dominance of taxonomic turnover over nestedness, functional nestedness and turnover contributed equally to the multiple-site β-diversity across elevations. The greater importance of functional nestedness compared to taxonomic nestedness is also reflected by pairwise β-diversity (Bishop et al., 2015). This implies that species-poor communities tend to maintain a subset of functional traits from species-rich communities of Collembola along the studied elevation gradient. Collembola species with similar morphological traits, such as body size and furca length, tend to occupy similar niches and this aligns with the assumption that functional redundancy buffers ecosystem processes against species loss, ensuring the persistence of key functions despite taxonomic changes (Petchey and Gaston, 2006). Moreover, the habitat nestedness hypothesis, which considers the nestedness of species assemblages to be due to the nested distribution of habitats (Wang et al., 2010), may apply to mountain regions with functional nestedness being more closely related to habitat nestedness than taxonomic nestedness along elevation gradients. These findings highlight the importance of integrating both taxonomic and functional dimensions when assessing biodiversity dynamics and conservation priorities along environmental gradients (Bishop et al., 2015).

The results indicated notable seasonal variation in the taxonomic and functional β-diversity of Collembola communities, with distinct patterns across different months. Taxonomic diversity increased with elevation in May and July, likely due to favorable environmental conditions such as warmer temperatures and increased plant productivity, which may enhance habitat availability and support diverse species (Ma et al., 2020). By contrast, functional β-diversity showed significant variation only in September, possibly reflecting shifts in resource availability after peak plant growth. Presumably, changes in litter decomposition rates and soil microbial activity toward the end of the growing season drive variations in functional traits of Collembola communities. These patterns highlight the differing sensitivities of species composition and functional traits to environmental gradients and emphasize the need to consider both taxonomic and functional diversity when assessing biodiversity (Nunes et al., 2016). Seasonal fluctuations in both also underscore the importance of a temporal perspective in understanding community responses to environmental changes.

4.2. Species and local contributions to taxonomic and functional β-diversity

The significantly higher taxonomic (both incidence-based and abundance-weighted) than functional β-diversity indicates that variations in Collembola community composition on Changbai Mountain are predominantly due to the variability in Collembola species rather than to the variability of their traits. This suggests that taxonomically distinct Collembola communities at different elevations possess similar functions pointing to functional redundancy (Ricotta et al., 2020). This indicates that despite changes in species identity with elevation, many species perform similar ecological roles, potentially stabilizing ecosystem functions under environmental change. Higher taxonomic than functional β-diversity pointing to functional redundancy has also been reported in fish and ant communities (Nakamura et al., 2020; Zhao et al., 2021).

The contribution of the site (in our case elevations) to incidence-based taxonomic β-diversity, i.e. the local contribution, followed a U-shaped pattern suggesting that the composition of Collembola communities at low and high elevations are more unique than those at medium elevations (Legendre and De Cáceres, 2013). Indeed, certain species, such as *Desoria* sp8, *Homidia* sp and *Bourletiella* sp3, were only found at the lowest elevation, whereas *Desoria tigrina* and *Desoria* sp5 were only found at higher elevations. Earlier studies on soil and canopy Collembola on Changbai Mountain also found the distribution of species to vary significantly with elevation with in particular middle elevations exhibiting higher proportions of locally abundant species than lower and higher elevations (Wu et al., 2023; Xie et al., 2022b)(Xie et al., 2022b) (Xie et al., 2022b). This suggests that species abundant at low and high elevations contribute most to β-diversity. However, the most important species contributing to β-diversity varied among incidence-based and abundance-weighted taxonomic as well as functional β-diversity among seasons. Yet, their contribution was generally low with the exception of *Isotomiella minor* which stood out as key species contributing 26 % to the abundance-weighted taxonomic β-diversity, reflecting its widespread distribution and high abundance. Generally, the higher species contribution to abundance-weighted than incidence-based β-diversity across seasons indicates that individual species reach high abundance at only few sites per season, presumably reflecting pronounced shifts in the structure and availability of resources with elevation and season (Legendre and De Cáceres, 2013).

4.3. Effects of environmental factors on β-diversity

Collembola communities on Changbai Mountain followed an elevation distance-decay relationship, a fundamental ecological principle quantifying the increase in compositional dissimilarity between communities with increasing elevational and environmental distance (Soininen et al., 2007). Similar relationships have been found for plants (Zhang et al., 2016), microorganisms (Kang et al., 2023; Shen et al., 2016), Enchytraeidae (Jiang et al., 2019) and mites (Lin et al., 2023) on Changbai Mountain. This underscores a pervasive pattern in changes in biodiversity along elevation gradients, highlighting the robustness of the distance-decay relationship across different organism groups and contributing to a broader understanding of community assembly mechanisms in montane environments.

Understanding the drivers of both taxonomic and functional β-diversity (and its components) is crucial for unveiling the mechanisms structuring biological communities (Dewan et al., 2022; Du et al., 2021; Zhou et al., 2022). Our results indicate that soil temperature and C/N ratio were the primary environmental drivers of β-diversity, while soil pH was of limited importance and did not exhibit a consistent main effect, which is conform to earlier studies on Collembola on Changbai Mountain (Xie et al., 2022b) and supports our third hypothesis.

For taxonomic β-diversity, the high explanatory power of environmental distance (up to 81 % of overall βsor) indicates that much of the compositional dissimilarity among communities can be attributed to environmental differences but this varies with season. Specifically, environmental distances explained more variation in Collembola in May and July than in September, likely due to seasonal variations in temperature, moisture and resource availability (Mehrafrooz Mayvan et al., 2022). In May and July, more extreme or variable conditions, such as warmer temperatures and fluctuating soil moisture, likely resulted in more pronounced differentiation in community structure (Wang et al., 2020). By contrast, more stable environmental conditions and maximum plant productivity in our study region in September may have diminished the impact of environmental factors (Yu et al., 2007). These results highlight the importance of considering seasonal variation when studying biodiversity and suggest that environmental gradients affect community structure differently depending on the time of year.

Notably, the species turnover component was strongly positively associated with increasing soil C/N ratio distances implying that species replacement is associated with variations in the quality of soil resources, supporting earlier suggestions that the assemblage of communities in mountain regions is related to nutrient regimes (Moses et al., 2023; Peters et al., 2014). Moreover, more pronounced differences in mean soil temperature were associated with increased taxonomic β-diversity and its components, emphasizing the overarching impact of temperature on the distribution of species (Makkonen et al., 2011; Salmon et al., 2014; Xie et al., 2022a). Notably, soil and air seasonal temperature explained different aspects of β-diversity. Soil seasonal temperature more strongly influenced nestedness than turnover, possibly indicating that communities experiencing similar seasonal fluctuations are more likely to share similar species. By contrast, air seasonal temperature was closely associated with both total β-diversity and its turnover component indicating that aboveground temperature fluctuations drive species replacement processes. Unexpectedly, soil pH correlated only weakly with incidence-based taxonomic β-diversity and its components, except for turnover in September, indicating that the influence of soil pH on Collembola community structure varies with season.

For abundance-weighted β-diversity, the full models of environmental distances explained considerably less of the total variation (37.0 %) compared to incidence-based taxonomic β-diversity (81.2 %). Specifically, total abundance-weighted β-diversity and its turnover component significantly increased, while the nestedness component significantly decreased with soil C/N ratio distances. By contrast, for incidence-based taxonomic β-diversity, only turnover significantly increased with soil C/N ratio distances, indicating that not only species presence-absence but also their abundances are influenced differently by environmental gradients. Overall, the results emphasize the importance of incorporating both incidence-based and abundance-based metrics when partitioning β-diversity (Anderson et al. 2011, Baselga 2013). Specifically, taking species abundance into account is crucial, as this improves uncovering the processes shaping changes in diversity along environmental gradients (Barwell et al. 2015, Janion-Scheepers et al. 2020, Zhao et al. 2021). In addition, as soil C/N ratio distance increased turnover also increased while nestedness declined, indicating a trade-off with the gain in species richness through turnover being offset by a decline in nestedness. This likely reflects different responses of dominant and rare species to resource gradients as demonstrated previously (Xie et al., 2022b).

Regarding functional β-diversity, a substantial fraction of the variation (up to 64 % for βsor) was explained by environmental distance. Notably, total functional β-diversity and its turnover component showed a significant increase with mean soil temperature distance, indicating that temperature differences across elevations are not only correlated with shifts in species composition but also actively drive the differentiation of functional traits across communities (Xie et al., 2022a). Additionally, soil pH was only positively correlated with functional β-diversity and its turnover component in September but not in May and July. This suggests that soil pH may become more influential in structuring communities near the end of the growing season in September. Previous studies showed that the body size of Collembola is associated with pH (Widenfalk et al., 2016; Xie et al., 2022a). This could be due to changes in soil microbial activity or shifts in microbial community structure, all of which may be more responsive to pH during this time (Han et al., 2018; Lux et al., 2022). Consequently, soil pH may serve as a stronger ecological filter in September, influencing both community composition and functional traits.

Functional β-diversity was calculated based on both effect and response traits of Collembola. However, the same trait may be linked to both environmental response and ecosystem effect (Lavorel and Garnier, 2002; Violle et al., 2007; Wright et al., 2016), making it difficult to strictly ascribe it to one of these categories. Faced with this difficulty and the fact that the function of traits often remains unknown the classification remains somewhat vague and this led some researchers to propose to replace it by more sophisticated metrics (Streit and Bellwood, 2023) which need closer consideration in future studies.

Overall, the findings emphasize the complex interplay of local habitat and climatic factors in shaping Collembola diversity along elevation gradients across seasons. Soil C/N ratio stands out as a pivotal driver of species turnover, complemented by the profound influence of mean soil temperature on both taxonomic and functional community assembly, but it varied between seasons. The observed disparity in the responses of incidence-based and abundance-weighted β-diversity to environmental gradients highlights the need for a multidimensional approach incorporating both taxonomic and functional aspects of diversity when investigating changes in community assembly along environmental gradients. Future studies may incorporate species-specific physiological tolerances and resource competition to enhance understanding of how environmental heterogeneity, particularly seasonal fluctuations, affects belowground biodiversity in mountain ecosystems.

4.4. Implications for conservation: The importance of specific elevations

Partitioning of β-diversity offers valuable insight for implementing effective conservation strategies. The dominance of the turnover component in total β-diversity across elevational bands is reminiscent of distinct species assemblages in isolated habitat fragments (Angeler, 2013; Zhao et al., 2021). This suggests that the conservation of Collembola in mountain regions, and presumably soil animal diversity in general, requires protection of habitats across altitudinal belts. This argues that, for implementing conservation strategies, partitioning β-diversity into turnover and nestedness components is needed. Considering both the contribution of species and elevation to taxonomic β-diversity, we found that lower and higher elevations contributed more to the variation in Collembola community composition, but these contributions fluctuated between seasons. This aligns with the principle that small, isolated patches are essential for the preservation of biodiversity (Lindenmayer, 2019), a viewpoint reinforced by a contemporary global *meta*-analysis highlighting their critical role for biodiversity conservation (Wintle et al., 2019). Additionally, implementing long-term monitoring programs to track seasonal changes in soil animal community composition will help to identify conservation measures to promote biodiversity in mountain ecosystems. Consequently, our results highlight the necessity of considering multiple β-diversity partitioning frameworks as well as seasonal variations when designing conservation strategies to preserve biodiversity in mountain ecosystems. Furthermore, both low and high elevation zones may serve as critical stepping stones, facilitating connection among geographically isolated regions. Enhanced connection of regions and dispersal may not only benefit Collembola, but also a wide range of taxa in particular those with restricted dispersal ability such as soil animals. Importantly, conservation strategies focusing on both high and low elevation zones facilitating the exchange of species and the flux of genes may ultimately fortify the resilience of mountain ecosystems.

CRediT authorship contribution statement

Zhijing Xie: Writing – review & editing, Writing – original draft, Software, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Jian Zhang:** Writing – review & editing, Software, Methodology, Investigation, Conceptualization. **Yuhao Zhao:** Writing – review & editing, Visualization, Software, Methodology. **Dingliang Xing:** Writing – review & editing, Visualization, Supervision, Software, Data curation, Conceptualization. **Yunga Wu:** Writing – review & editing, Methodology, Investigation, Data curation. **Johannes Lux:** Writing – review & editing, Visualization, Software, Data curation. **Liang Chang:** Writing – review & editing, Writing – original draft, Validation, Investigation, Conceptualization. **Kangle Lu:** Writing – review & editing, Visualization, Methodology, Investigation, Data curation, Conceptualization. **Xin Sun:** Writing – review & editing, Writing – original draft, Visualization, Data curation, Conceptualization. **Donghui Wu:** Writing – review & editing, Visualization, Validation, Supervision, Project administration, Investigation, Funding acquisition, Conceptualization. **Stefan Scheu:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Project administration, Investigation, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

This work was supported by the National Natural Science Foundation of China (42301072), National Science & Technology Fundamental Resources Investigation Program of China (2024FY100400), the Fundamental Research Funds for the Central Universities (2412023QD028) and the Program of Introducing Talents of Discipline to Universities (No. B16011). We express our sincere thanks to Louis Deharveng and Anne Bedos from Muséum National d'Histoire Naturelle, Sorbonne Université, Mikhail Potapov from Moscow State Pedagogical University for help with the identification of species. We also thank Zheng Zhou, Xue Pan and Ting-wen Chen for helpful suggestions on the manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.geoderma.2025.117322.

Data availability

Data associated with this study are available from the Dryad Digital Repository: http://datadryad.org/stash/share/6fWpBEa9_LpJko50I-D4r1EKccLive83jD-_6kBjr0g4

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