



Elevational changes in canopy Collembola community composition are primarily driven by species turnover on Changbai Mountain, northeastern China

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Abstract

Forest canopies harbor extraordinary biodiversity, with Collembola being one of the most abundant arthropod taxa. However, much of the research on canopy biodiversity has focused on tropical and subtropical regions, leaving a gap in our understanding of canopy communities in temperate and boreal forests. Studying canopy Collembola along elevational gradients can be particularly informative because several environmental factors change with elevation, and these changes may mirror those seen along latitudinal gradients. To better understand and conserve canopy Collembola diversity along elevational gradients, natural forests are of particular interest. In this study, we used canopy fogging to sample canopy Collembola at four elevation sites (800–1700 m a.s.l.) on Changbai Mountain, northeastern China, representing three natural forest types. We examined changes in species richness, abundance and composition of canopy Collembola, and partitioned beta diversity into nestedness and turnover to identify processes driving changes in community composition. We identified 53 morphospecies among 10,191 individuals, with Entomobryidae and Hypogastruridae being the dominant families. The highest abundance and species richness were observed at 1400 m and remained at similar levels at 1700 m, indicating an increasing pattern with elevation. Species turnover was the main driver of changes in community composition with elevation. Our results provide insights into the shift of canopy Collembola communities across an elevational gradient in temperate boreal forests.

Keywords Canopy fauna · Mountain biodiversity · Altitudinal gradient · Arthropods · Canopy fogging · Beta-diversity

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Introduction

Identifying spatial patterns in biological communities has been a major theme in ecology over the past century, and inferring community assembly processes underlying the patterns provides a mechanistic understanding of changes in biodiversity in the face of environmental changes (Jackson and Blois 2015). Due to steep changes in both abiotic and biotic factors (Rahbek et al. 2019a), elevational gradients in mountains have been identified as natural experiments that allow the identification of drivers of biodiversity change across biomes, such as climatic factors and vegetation (Cheng et al. 2023). Among aboveground habitats, forest canopies are exceptionally species-rich, with biodiversity even exceeding that of the understory and the soil stratum (Stork et al. 2015). However, the biodiversity of forest canopies is relatively understudied, especially for arthropods living in this stratum in natural forests (Novotny et al. 2002; Hsieh and Linsenmair 2011), which are particularly diverse and form an essential component of canopy food web (Hamilton et al. 2010). Canopy arthropods span multiple trophic levels (Basset et al. 2003), yet previous studies have predominantly focused on herbivores and predators, with insufficient attention directed towards detritivores. Forest canopies serve as critical engines of global biogeochemical processes, forming a dynamic interface between the terrestrial biosphere and the atmosphere (Ozanne et al. 2003). Ecologists have emphasized the importance of studying forest canopy fauna to understand biodiversity at local and global scales, and to inform conservation management (Stork 2001; Nakamura et al. 2017).

Canopy arthropods are dominated by insects, with Collembola being one of the most abundant taxa and most important detritivores (Basset et al. 2012). Investigating the distribution of Collembola species in tree canopies along elevational gradients is crucial for understanding the canopy arthropod food web and its response to environmental change. Collembola are among the most abundant and widespread microarthropods in terrestrial ecosystems. They function as important soil and litter decomposers (Deharveng 2004), but they are also abundant in the tree canopies, in some cases accounting for up to 95% of total arthropod abundance (Palacios-Vargas et al. 1998; Mawan et al. 2022). Canopy Collembola play an important role in the canopy food web by functioning as detritivores (Yoshida and Hijii 2005a), but also by serving as prey for predatory arthropods (Halaj et al. 1998; Rozanova et al. 2021). Recent research in tropical rainforests suggests that they live predominantly as algae-microbivores and may contribute substantially to the overall energy flux in canopy food webs (Pollierer et al. 2023). In addition, Collembola are sensitive to environmental changes, making them an ideal model group for studying community changes across elevations and between forests of different composition. Early studies showed that canopy Collembola diversity varies with forest type (Guilbert et al. 1993; Basset 2001). However, existing studies are concentrated within tropical and subtropical regions, whereas canopy Collembola of temperate and boreal zones have received little attention, with existing studies conducted in plantation forests (Yoshida and Hijii 2005a, 2014).

Mountain and high-elevation regions are among the most vulnerable ecosystems to global climate change and their biodiversity is expected to decline significantly in the near future (La Sorte and Jetz 2010; Pepin et al. 2015). Changes in biodiversity with elevation can vary among taxa and may decrease monotonically, remain unchanged, increase, or follow a hump-shaped pattern (Rahbek 1995; Wrenkraut and Ruggiero 2014; Chen et al. 2020). A number of studies have reported a hump-shaped pattern of biodiversity along

elevational gradients (Rahbek 1995; Sanders and Rahbek 2012), often attributed to climate constraints such as temperature limitation at higher elevations and precipitation limitation at lower elevations (Supriya et al. 2019; Uhey et al. 2021). Beyond these climate constraints, mid-elevation dominance has also been linked to dispersal constraints and the mid-domain effect based on species distribution ranges (Colwell and Lees 2000; McCain 2004). Elevational changes in diversity have been linked to a wide range of environmental factors (McCain et al. 2018), therefore, species diversity patterns along elevational gradients may provide important insights into the processes driving community assembly at broad spatial scales (Sang and Bai 2009; Beck et al. 2017; Abutaha et al. 2019). We investigated the patterns of canopy Collembola diversity, abundance, richness and composition along elevational gradient on Changbai Mountain, China, located in the temperate zone of the Northern Hemisphere. Changbai Mountain is one of the largest protected forests in the world and is of outstanding importance for biodiversity conservation (Yang and Xu 2003). Following the climatic gradient along the mountain slope, Changbai Mountain is characterized by a clear vertical zonation of vegetation (Zhao et al. 2004). Across this distinct elevational gradient, the diversity patterns of soil Collembola were found to follow either a hump-shaped pattern or a monotonic increase, depending on the Collembola groups studied (Sun et al. 2020; Xie et al. 2022b).

Species diversity patterns along elevational gradients can provide important insights into the processes driving community assembly (McCain and Grytnes 2010; Rahbek et al. 2019b). Here, in addition to previous studies (Sun et al. 2020; Xie et al. 2022a, b), we examined beta diversity, a measure of the difference in species composition either between local assemblages or between local and regional assemblages (Whittaker 1972; Koleff et al. 2003). Analysis of beta diversity can reveal general patterns and underlying mechanisms of elevational changes in biodiversity (Socolar et al. 2016). Statistically, beta diversity can be partitioned into two components, i.e. species turnover (or replacement) and nestedness (Harrison et al. 1992; Legendre 2014; Zhao et al. 2021). Species turnover reflects the replacement of existing species by different species at new sites, while nestedness quantifies the degree of species identity between sites (Baselga 2010). If environmental conditions vary between sites and species are adapted to particular conditions, species turnover is likely to dominate community shifts, i.e. local communities are structured mainly by environmental filtering. In addition, spatial and historical constraints can lead to a pattern of species turnover (Qian et al. 2005). For instance, prolonged isolation and diverse geography can lead to a high rates of species turnover, as observed in soil Collembola (Janion-Scheepers et al. 2020). On the other hand, nestedness can result from selective colonization, selective extinction, habitat nestedness, or passive sampling (Wang et al. 2010). Therefore, analyzing the relationship between beta diversity components can provide a better understanding of community assembly processes (Fattorini 2009; Wu et al. 2017; Zhao et al. 2021).

In this study, we investigated canopy Collembola assemblages and their beta diversity components along an elevation gradient on Changbai Mountain, thus forming three hypotheses:

- (i) the peak of abundance and species richness occurs at mid-elevation (1400 m), approximately halfway between the mountain base (720 m) and the tree line (2000 m), exhibiting a hump-shaped pattern with elevation,
- (ii) the community composition of canopy Collembola varies with forest type,

- (iii) changes in canopy Collembola communities with elevation are mainly due to species turnover, i.e. environmental filtering is the predominant driving force of beta diversity.

Material & methods

Study area

Samples were collected within the Changbaishan Nature Reserve (hereafter Changbai Mountain), northeastern China (41°41'–42°51' N; 127°43'–128°16' E). The reserve covers approximately 200,000 ha, and its elevation ranges from 720 to 2691 m (Yang and Xu 2003). The area experiences a temperate continental monsoon climate, with pronounced changes in temperature and precipitation with increasing elevation (Zhang et al. 2015). Mean annual precipitation ranges from 750 to 1340 mm, with most of the precipitation occurring between June and September (Wang et al. 2013b).

Changbai Mountain is characterized by a clear elevational zonation of the vegetation, especially along the northern slope (Zhao et al. 2004; Sang and Bai 2009; Bai et al. 2011). Four forest types along the elevation gradient were selected for this study: (1) Mixed coniferous and broad-leaved forest at 800 m; mean annual temperature is 2.7 °C and mean annual precipitation is 683 mm. Tree species are dominated by *Pinus koraiensis*, *Tilia amurensis*, *Fraxinus mandshurica* and *Acer mono*. (2) Mixed coniferous forest at 1100 m; mean annual temperature is 1.6 °C and mean annual precipitation is 762 mm. Tree species are dominated by *Pinus koraiensis*, *Fraxinus mandshurica* and other broad-leaved trees and conifers such as *Picea jezoensis*, *Abies nephrolepis* and *Larix olgensis*. (3) Sub-alpine coniferous forest at 1400 m; mean annual temperature is -0.6 °C and mean annual precipitation is 809 mm. Tree species are dominated by *Picea jezoensis* and *Abies nephrolepis*. Except for these dominant conifer species, *Acer* spp., *Populus* spp., *Betula costata*, *B. ermanii* and *Sorbus pohuashanensis* are interspersed. (4) Sub-alpine coniferous forest at 1700 m; mean annual temperature is -1.7 °C and mean annual precipitation is 880 mm. The forest is also dominated by *Picea jezoensis* and *Abies nephrolepis*, but additional species comprise predominantly *Betula platyphylla* and *Sorbus mandshurica*.

Sampling of canopy arthropods

In August 2016, canopy arthropod samples were collected using canopy fogging as described in detail in Zheng et al. (2015). At each elevation, we visually identified four representative plots containing canopies of the dominant tree species. The four plots were spaced by 30 m (Fig. S1). We suspended 100 traps with a diameter of 1 m at a height of approximately 1.5 m above the ground in each plot, resulting in a total of 400 subsamples per elevation and a total of 1600 subsamples across the four elevations. A 50 ml vessel filled with 25 ml of 95% ethanol was fitted to the bottom of each trap. Fogging began before daybreak when the wind speed was lowest to minimize fog scatter. We avoided sampling after rain or during windy or misty conditions. For fogging, we used 2 L of a 2.2% pyrethroid solution dissolved in diesel oil. This dosage has been proven effective in arthropod extermination while exhibit-

ing low toxicity for vertebrates (Stork and Hammond 1997). The insecticide was applied for approximately 30 min, which was sufficient to reach the entire canopy. After 3 h invertebrates which dropped onto the traps were directed to the center of the traps and collected in the vessels with ethanol.

For this study, we combined 12 randomly selected subsamples from the 100 subsamples per plot into one sample. This resulted in 4 replicate samples per elevation and a total of 16 samples across the four elevations. Canopy Collembola were sorted under a stereomicroscope (SMZ745T, Nikon, Japan) and ascribed to three orders according to the protocol of Deharveng (2004) and the Checklist of Collembola of the world (<http://collembola.org/>). For species/morphospecies determination, Collembola were inspected under microscope (Eclipse 80i, Nikon, Japan) using relevant publications (Jia et al. 2010; Wang et al. 2013a).

Statistical analysis

All statistical analyses were performed in the R environment (v. 4.2.2; R Core Team, 2019) and visualized using the “ggplot2” package. Species accumulation curves were computed using the “specaccum” function in the “vegan” package (Oksanen et al. 2022). We used the “iNEXT” package (Hsieh et al. 2016) to plot individual-based sample completeness curves for the four elevations and the associated 95% unconditioned confidence intervals (Fig. S2).

Abundance data were $\log(x+1)$ transformed to meet the assumptions of normality and homogeneity of variance. We used the “lm” function to analyze the effects of elevation on canopy Collembola abundance, species richness, Shannon-Wiener index, Simpson index and Pielou index, and the “anova” function to perform Chi-square-tests. Means between elevations were compared using Tukey’s honestly significant difference (HSD) function from the “stats” package. To facilitate interpretation, means and standard errors were back-transformed for graphical presentation. Principal co-ordinates analysis (PCoA) (vegan::pcoa) based on pairwise Bray-Curtis distance was performed to analyze differences in Collembola community composition between elevations. In addition, differences in community composition were analyzed using permutational manova (PERMANOVA) (vegan::adonis). Venn diagrams were drawn using the “VennDiagram” package (Chen 2022).

Beta diversity was partitioned into turnover and nestedness using the “betapart” package (Baselga and Orme 2012). Presence/absence data were used for multisite taxonomic dissimilarity partitioning (Baselga 2010). Community dissimilarity matrices were generated for total beta diversity using the Sorensen index (β_{sor}) and its additive components: turnover (Simpson index, β_{sim}) and nestedness (β_{sne}). For partitioning abundance-weighted beta diversity, we used the multisite and pairwise dissimilarity partitioning approaches proposed by Baselga (2013). Overall abundance-weighted beta diversity (i.e., β_{bray}) was also partitioned into two components, i.e. balanced variation in abundance (β_{bal}) and abundance gradients (β_{gra}). The abundance framework is analogous to the partitioning of beta diversity into spatial turnover and nestedness. Thus, β_{bal} and β_{gra} represent abundance turnover and abundance nestedness, respectively (Loiseau et al. 2017; Zhao et al. 2021). In addition, similarity percentages (SIMPER) analyses were performed to determine the contribution of species to the average pairwise Bray-Curtis dissimilarity between elevations (Clarke 1993).

Results

In total, 10,191 individuals of Collembola were collected, representing 3 orders, 10 families and 53 morphospecies (Supplementary material, Table S1). The species accumulation curve of the pooled 192 traps flattened and reached a limit at the total of 53 species (Fig. S3), indicating that our sampling represents the complete Collembola community at the studied mountain gradient at that time.

Species richness-elevation relationship and abundance-elevation relationship

Both average abundance and species richness varied significantly with elevation (LM, $F_{(3, 12)}=7.39, p<0.001$, $F_{(3, 12)}=9.61, p<0.01$, respectively). Average abundance increased from 800 (199.3 ± 84.19) to 1100 (340.5 ± 67.98) to 1400 m (1089.5 ± 925.60) and then remained at a similar level at 1700 m (918.5 ± 557.65) (Fig. 1a). Average species richness was similar at 800 m (13.0 ± 1.4) and 1100 m (13.8 ± 1.3) and then increased to a similar levels at 1400 m (20.0 ± 2.83) and 1700 m (17.5 ± 2.52) (Fig. 1b). In contrast, elevation did not significantly affect the Shannon-Wiener, Simpson and Pielou indices (data not shown), indicating a limited effect of elevation on canopy Collembola diversity and evenness. Different Collembola families showed different responses to elevation (LM, $F_{(3, 12)}=1.72, p<0.05$; Fig. S4). Specifically, Hypogastruridae, Tomoceridae, Sminthuridae, Isotomidae and Neanuridae significantly increasing in abundance in response to elevation. In contrast, the average abundance of Entomobryidae, Sminthurididae, and Katiannidae remained relatively constant across elevations.

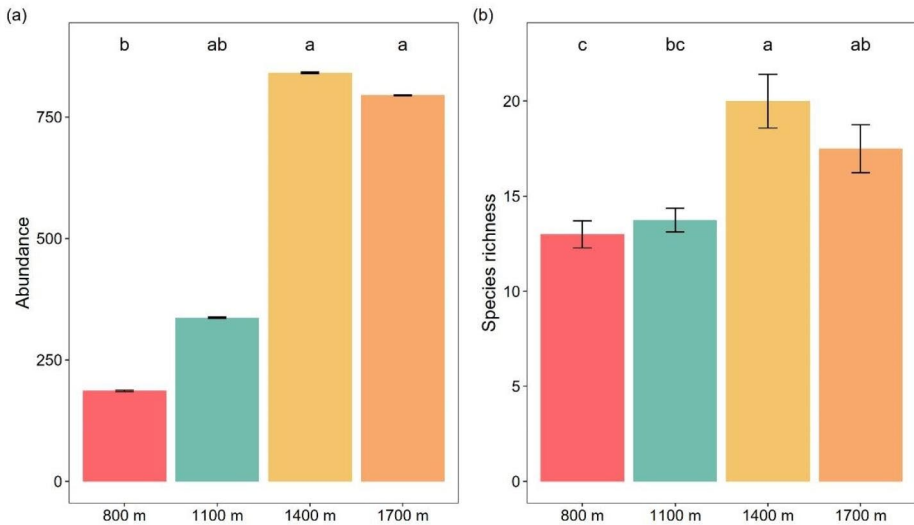


Fig. 1 Mean abundance \pm standard error (a) and mean species richness \pm standard error (b) of canopy Collembola at four elevations on Changbai Mountain; back-transformed means and standard errors of log-transformed data. Different letters indicate significant differences between elevations (Tukey's HSD test, $p<0.05$)

Community composition

PCoA based on pairwise Bray-Curtis distance revealed a distinct composition of canopy Collembola communities, separating them into three groups, i.e. sites at 800, 1100 as well as 1400 and 1700 m combined (PERMANOVA, $F_{(3, 12)}=8.59$, $p<0.001$; Fig. 2a). The distinctness of the communities at 800 m is also reflected by the fact that 11 species occurred only at this site (Fig. 2b, Table S2). The intermediate position of the 1100 m site is also reflected by 10 species overlapping with the site at 800 m and 12 species overlapping with the sites at 1400 and 1700 m, with only 2 species only occurring at 1100 m. The sites at 1400 and 1700 m shared 20 species, with 6 and 3 species occurring only at 1400 and 1700 m, respectively.

Generally, Entomobryidae and Hypogastruridae were the dominant families accounting for 36.0% and 28.6% of the total canopy Collembola abundance, respectively (Fig. 3). At 800, 1100 and 1700 m, Entomobryidae dominated (89.8%, 74.0% and 30.9% respectively), with the second most abundant families being Tomoceridae (3.51%) at 800 m and Hypogastruridae (15.4%) at 1100 m. At 1400 m Hypogastruridae (50.3%) dominated followed by Tomoceridae (22.5%). At 1700 m the family composition was more balanced with similar contributions from Entomobryidae (30.9%) and Sminthuridae (29.5%) and lower contributions from Hypogastruridae (13.4%) and Tomoceridae (11.1%).

Species turnover and nestedness

Generally, the turnover component (β_{sim} and β_{bal}) of beta diversity dominated, contributing 91.2% and 81.8% to the incidence-based and abundance-weighted total beta diversity, respectively (Fig. 4). This was also true for the pairwise comparison of elevations, the turnover component (balanced variation in abundance) contributed 87.0%, 95.0% and 98.2% to total Bray-Curtis beta diversity between 800 and 1100 m, 800 and 1400 m, and 800 and 1700 m, respectively. The contribution of the nestedness component (unidirectional abundance gradient) to beta diversity was higher for pairwise comparisons between 1100

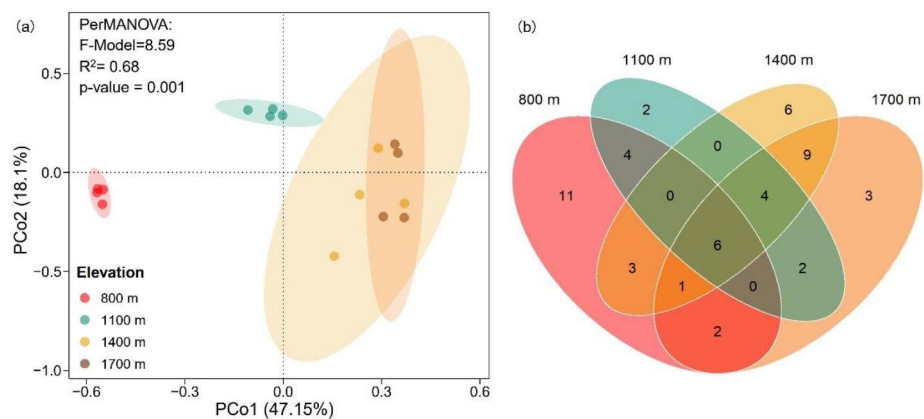


Fig. 2 Community composition of canopy Collembola on Changbai Mountain as indicated by principal coordinate analysis (PCoA) (a) and the overlap of species between the four elevations studied (b)

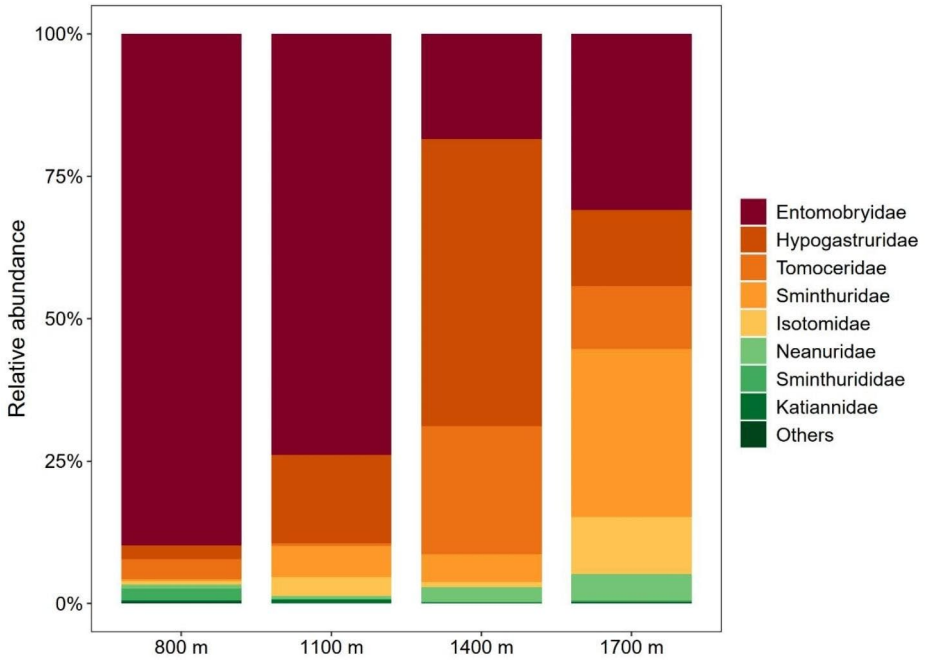


Fig. 3 Relative abundance of canopy Collembola families at four elevations on Changbai Mountain

Fig. 4 The relative contributions of spatial turnover (β_{sim}) and nestedness (β_{sne}) components of total taxonomic (both incidence-based and abundance-weighted) β diversity among four elevations on Changbai Mountain. The β_{ratio} was the ratio between the value of turnover and the value of overall multiple-site β diversity

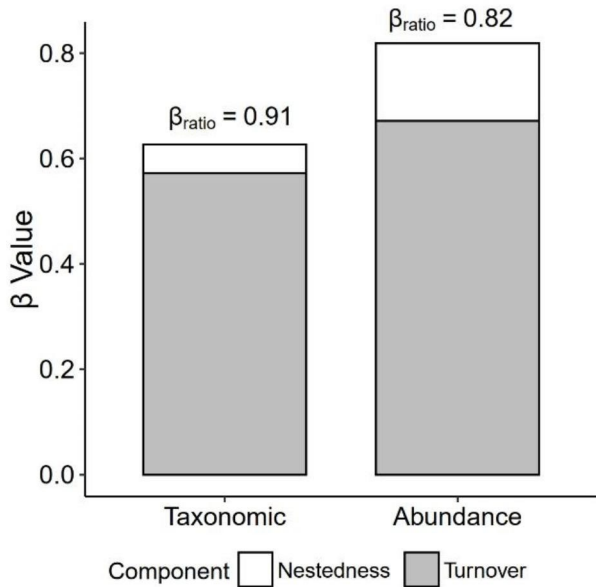


Table 1 Pairwise distance matrix for the abundance-based partitioning of pairwise Bray-Curtis dissimilarity, with spatial turnover measured as balanced variation in abundance between elevations (β_{bal}) (bold) and nestedness measured as the unidirectional abundance gradients between elevations (β_{gra}) (unbold) between Collembola communities of different elevations on Changbai Mountain. The percentage contribution to total beta diversity is given in parentheses

	800 m	1100 m	1400 m	1700 m
800 m		0.095 (13.0%)	0.049 (5.0%)	0.018 (1.8%)
1100 m	0.637 (87.0%)		0.281 (37.8%)	0.280 (41.8%)
1400 m	0.930 (95.0%)	0.463 (62.2%)		0.034 (5.4%)
1700 m	0.972 (98.2%)	0.390 (58.2%)	0.599 (94.6%)	

Table 2 Analysis of similarity (SIMPER) of Collembola families and the three most abundant species contributing to the dissimilarity of Collembola communities between elevations. Av_a and Av_b represent the average abundance of Collembola at the respective two elevations compared. Only families contributing >10% to the community difference are shown

	Taxa	Contribution (%)	Av_a (ind./sample)	Av_b (ind./sample)	P value
Family					
800 m vs. 1100 m	Entomobryidae	17.75	179.0	252.0	0.033
800 m vs. 1400 m	Tomoceridae	23.67	7.0	245.5	0.001
800 m vs. 1700 m	Sminthuridae	22.29	0.8	271.0	0.001
1100 m vs. 1400 m	Tomoceridae	20.79	1.8	245.5	0.004
1100 m vs. 1700 m	Sminthuridae	17.83	18.8	271.0	0.002
Species					
800 m vs. 1100 m	<i>Entomobrya</i> sp.4	23.31	0	122.0	0.004
	<i>Entomobrya</i> sp.8	17.56	98.8	0	0.001
	<i>Entomobrya</i> sp.1	8.02	51.0	91.0	0.028
800 m vs. 1400 m	Tomoceridae sp.1	24.21	0	242.8	0.001
	Hypogastruridae sp.7	15.95	0.5	404.8	0.001
	Xenylla sp.1	3.84	0	75.0	0.001
800 m vs. 1700 m	<i>Entomobrya</i> sp.4	22.91	0	278.5	0.002
	Sminthuridae sp.1	22.03	0.3	266.8	0.001
	Isotomidae sp.4	5.18	0	69.3	0.001
1100 m vs. 1400 m	Tomoceridae sp.1	20.78	0	242.8	0.003
	Hypogastruridae sp.7	15.06	0.5	404.8	0.031
	Entomobrya sp.1	7.68	91.0	8.0	0.038
1100 m vs. 1700 m	Sminthuridae sp.1	17.55	18.8	266.8	0.002
	<i>Entomobrya</i> sp.1	8.28	91.0	2.5	0.015
	Isotomidae sp.4	4.58	0	69.3	0.005

and 1400 m, and 1100 and 1700 m, accounting for 37.8% and 41.8% of total beta diversity, respectively (Table 1).

As indicated by SIMPER analysis, Entomobryidae, Tomoceridae and Sminthuridae contributed significantly to the dissimilarity between elevations (Table 2). The families contributing most to community dissimilarity were Entomobryidae between 800 and 1100 m (17.8% of the total dissimilarity), Tomoceridae between 800 and 1400 m (23.7%), Sminthuridae between 800 and 1700 m (22.3%), Tomoceridae between 1100 and 1400 m (20.8%) and Sminthuridae between 1100 and 1700 m (17.8%).

At the species level, the increase in abundance of *Entomobrya* sp.4 strongly contributed to the dissimilarity between 800 m and higher elevations. Dissimilarities between 1100 m and the other three elevations were mainly due to decreased abundance of *Entomobrya* sp.1. Dissimilarities between 1400 m and the other elevations were mainly due to increased abundance of Tomoceridae sp.1 and Hypogastruridae sp.7. Most of the species contributing significantly to community dissimilarity between elevations were dominant at least one of the elevations, except for Isotomidae sp.4 (Fig. S5).

Discussion

To the best of our knowledge, this is the first study to analyze elevational diversity patterns of canopy Collembola in natural deciduous and coniferous forests. The results demonstrate that both species richness and abundance of Collembola increase with elevation at the site and these changes are associated with pronounced changes in Collembola community composition driven by species turnover. Importantly, our sampling was conducted during the typical rainy growing season on Changbai Mountain, and prior research in tropical forests indicates that canopy Collembola are most abundant during the rainy season (Tovar-Sánchez et al. 2004; Palacios-Vargas et al. 2021). In part, this may be due to the movement of soil-dwelling Collembola into the canopy (Yoshida and Hijii 2005a). For soil Collembola on Changbai Mountain, precipitation seasonality also has been found to be a major driver of abundance and community composition (Xie et al. 2022b). In addition, Yoshida and Hijii (2006) reported that sampling in growing season sampling yielded more litter-dwelling Collembola species. Hence, our sampling likely well represents the canopy Collembola community, although it may not have captured the full spectrum of species. Interestingly, the abundance of canopy Collembola was much lower than that of soil Collembola on Changbai Mountain (Xie et al. 2022b). However, earlier investigations have suggested that the abundance of Collembola in canopy leaf litter and suspended soil exceeds that in forest floor litter and soil (Yoshida and Hijii 2005a; Alviola et al. 2020). At least in part, this may be due to different sampling methodologies. However, despite the rather low abundance of canopy Collembola in our study, species richness (53) was higher than seen in previous studies (Rodgers and Kitching 2011; Alviola et al. 2020) suggesting that canopy fogging effectively captures canopy Collembola.

Changes in abundance and species richness with elevation

Contrary to our first hypothesis of a hump-shaped pattern of canopy Collembola abundance along the elevational gradient studied, the mean abundance of canopy Collembola increased with elevation, indicating more beneficial environmental conditions at higher elevations. This pattern contrasts that of soil Collembola which remained at similar densities in forests at higher elevations (Xie et al. 2022b), supporting the “arboreality hypothesis,” i.e. increased colonization of trees with increasing elevation observed e.g., in frogs (Scheffers et al. 2013). Increased arboreality of canopy Collembola abundance with elevation has also been documented at lower elevation gradients (442–900 m) in the Philippines from forest floor soil to canopy suspended soil (Alviola et al. 2020). An increase in arboreality is likely related to increased precipitation with elevation. Our sampling was conducted in August, a month characterized by high precipitation on Changbai Mountain (Wang et al. 2013b),

and precipitation has been shown to drive canopy colonization by Collembola (Farrow and Greenslade 1992; Yoshida and Hiji 2005a). Furthermore, canopy spiders, which are the primary predators of Collembola (Halaj et al. 1998), decrease in abundance with increasing elevation on Changbai Mountain (Zhao 2019), potentially contributing to increased Collembola abundance due to reduced predation pressure.

Similar to abundance, canopy Collembola species richness did not follow a hump-shaped pattern along the studied elevation gradient, but also increased with elevation, again disproving our first hypothesis. The pattern, however, is in contrast to Collembola species richness in the soil or in mosses on the tree bark, which have been shown to decrease with elevation (Cutz-Pool et al. 2010; Bokhorst et al. 2018). Again, as in abundance, beneficial moisture conditions likely contributed to the increase in species richness at higher elevations. Increases in abundance and species richness with elevation have also been observed for other taxa, such as plants and vertebrates, however, the factors responsible for these changes are likely different. Further, changes in elevation may be influenced by the elevation range sampled (Mena and Vázquez-Domínguez 2005; Dani et al. 2023). Our highest elevation point at 1700 m was below the tree line (2000 m), potentially introducing some bias in the observed elevational pattern of canopy Collembola. However, canopy Collembola communities are naturally restricted to forests.

In addition to changes in moisture and temperature with elevation, changes in the abundance and species richness of canopy Collembola with elevation are also likely related to changes in tree species and forest type (Basset 2001). Tree species identity and forest type are important drivers of the composition, abundance, and richness of both above- and belowground fauna. Zhang et al. (2012) found that forest type drove soil nematode abundance along elevational gradients, and Zou et al. (2014) found that changes in ground beetle abundance with elevation were associated with the distribution of Korean pine. On the northern slope of Changbai Mountain, tree density increases with elevation and shifts from deciduous to coniferous dominance at higher elevations (1400 and 1700 m). Thus, the changes we observe in canopy Collembola with elevation also are likely related to the concurrent changes in tree species and the associated microhabitats and resources (Illig et al. 2010; Bokhorst et al. 2018; Alviola et al. 2020). To note, epiphytes are typically rare in the canopy of forests on Changbai Mountain and therefore likely play a minor role (Liu 1997; Guo and Cao 2012). The higher abundance and species richness at higher conifer-dominated elevations on Changbai Mountain can be attributed to the fact that deciduous trees shed their leaves in winter, creating less stable habitat, whereas conifers retain their needles year-round, providing a more consistent environment for Collembola colonization. In addition, the typically more structured bark microhabitats of coniferous than broad-leaved trees (Zhao et al. 2004) may have contributed to the higher abundance and species richness of canopy Collembola at higher elevations. Further, slower decomposition may support higher Collembola abundances (Kitching et al. 1993), and therefore slower decomposition of conifer needles compared to leaves of deciduous leaves (Guo et al. 2007), as well as the generally slower decomposition of litter at higher elevations (Zhou et al. 2015) may have contributed to the higher abundance and species richness at higher elevations.

In soil, higher densities of Collembola in coniferous forests compared to deciduous forests have been suggested to be due to more habitable space in the former due to thicker litter layers (Pollierer and Scheu 2017; Kuznetsova et al. 2018). Collembola in the canopy may be directly related to Collembola in the soil, as some species migrate between soil and canopy (Leinaas 1983; Yoshida and Hiji 2006). In Australian forests, up to half of the Collembola

species it has been reported be shared between soil and canopy (Greenslade and Deharveng 1990; Rodgers and Kitching 1998). Similarly, canopy and soil communities in Japanese forests have been shown to share dominant Collembola species (Yoshida and Hijii 2005a, 2006), which is also the case on Changbai Mountain (Jia et al. 2010; Wang et al. 2013a). Species of other arthropod taxa, such as beetles, ants and mites have also been shown to colonize both the canopy and the soil (Nadkarni and Longino 1990). However, as with most arthropod taxa (Rodgers and Kitching 1998), a number of Collembola species colonize the canopy exclusively (Greenslade 1994; Ozanne 1999; Greenslade et al. 2016). Overall, our results and previous findings suggest a close link between the canopy and soil fauna, suggesting that the forest canopy should not be studied in isolation. Rather, more attention should be paid to better understanding the relationships between the canopy and soil fauna, and the associated interactions between the above- and belowground systems.

Changes in species composition with elevation

Generally, canopy Collembola communities were dominated by Entomobryidae and Hypogastruridae. The dominance of Entomobryidae is likely related to their epedaphic life form (living on or above the ground), wide distribution and high species richness (Zhang et al. 2014). The dominance of epedaphic Collembola is consistent with previous findings that canopy Collembola are primarily composed of epedaphic species (Guilbert et al. 1995; Palacios-Vargas et al. 1998). Similar to our study, Entomobryidae were also found to be the dominant family of Collembola in the canopy of Australian rainforests (Greenslade et al. 2016) and boreal forests of Norway (Thunes et al. 2003). Further, Mawan et al. (2022) also found Entomobryidae to be among the most dominant Collembola across rainforests and plantation forests in Indonesia. Compared to lower elevations (800 and 1100 m), canopy Collembola at 1400 m were dominated by Hypogastruridae, which contributed more than 50% of the total abundance. Notably, a single species, Hypogastruridae sp.7, accounted for 74% of all Hypogastruridae individuals. Similarly Yoshida and Hijii (2005b) also found that Hypogastruridae to dominate Collembola communities in the canopy of *Cryptomeria japonica* plantations in Japan, with one species accounting for the majority of Collembola abundance. This suggests that Hypogastruridae comprise opportunistic species capable of rapid population growth in the canopy of trees, but also that they require specific environmental conditions present only in a narrow range of forest types (Coleman et al. 2004). Although the majority of the reported canopy Collembola species are epedaphic, a smaller portion comprises hemi-edaphic species, including Hypogastruridae, Neanuridae and Odontellidae. Notably, Sminthurididae have not been reported from the soil fauna of Changbai Mountain suggesting that the Sminthurididae species encountered in our samples may be specialized in colonizing the canopy.

Changes in canopy Collembola community composition with elevation were associated with changes in forest type, supporting our second hypothesis. The mixture of coniferous and broad-leaved trees at 800 m and the associated high habitat heterogeneity likely contributed to the distinct Collembola community composition at this elevation. This pattern is also observed in soil arthropod communities, which have also been shown to differ between broad-leaved and coniferous stands (Korboulewsky et al. 2016, 2021). The presence of both broad-leaved and coniferous tree species at 800 m may also have contributed to the large number of Collembola species occurring only at this elevation. The close association of Collembola species with a particular forest type is also indicated by the large overlap of canopy Collembola species at 1400 and 1700 m, where the same tree species dominate. This pattern

is consistent with that of soil Collembola and also soil oribatid mites (Xie et al. 2022b; Liu et al. 2023). Thus, it is clear that community shifts are often the result of a complex interplay of environmental factors, including temperature, precipitation, and habitat (Maunsell et al. 2013). Here, the elevational changes in climate have a strong impact on tree composition, which then likely drives subsequent shifts in Collembola, thus these factors are intertwined and warrant further attention in future studies.

Species turnover and nestedness between elevations

Supporting our third hypothesis, changes in canopy Collembola community composition with elevation were mainly driven by species turnover rather than nestedness. The dominance of species turnover in community composition changes with elevation has also been reported for soil mites (Liu et al. 2023a), soil enchytraeids (Jiang et al. 2019), ants, birds and rodents (Wang et al. 2012; Du et al. 2021). There are two hypotheses regarding the relationship between species turnover and elevation. First, species turnover with elevation may be related to species richness, i.e. it may be more pronounced in regions of high diversity (Lomolino 2001; Fattorini 2014). Second, it may also be related to changes in species range size with elevation. Rapoport's rule stipulates that species at higher latitudes possess wider latitudinal ranges compared to those at lower latitudes (Rapoport 1982; Stevens 1989). This phenomenon may also apply to elevational gradients, where species at higher elevations tend to have larger elevational ranges resulting in lower species turnover (Stevens 1992). Supporting the latter, canopy Collembola species richness on Changbai Mountain was maximized at 1400 and 1700 m, with low species turnover between these two elevations. Similar patterns have also been observed for vertebrates (Lennon et al. 2001; McCain and Beck 2016).

Overall, our results suggest that species turnover plays the most pivotal role in driving changes in the canopy Collembola community composition along elevational gradients. The consistent pattern observed across different mountain regions implies that elevational bands within mountain ranges tend to harbor distinct animal communities, rather than communities thinning out at higher elevations. Within the canopy, Collembola likely serve as important prey for a range of predators including spiders, ants and staphylinid beetles. This underscores the importance of mountains as reservoirs of biodiversity due to the elevation-based species turnover (Bishop et al. 2015). As predicted by global climate change, species distributions are shifting towards mountain summits (Yu et al. 2014; Du et al. 2018). Upward shifts in the tree line and the associated shrinking of habitat space therefore pose a threat to canopy Collembola and other high-elevation species (Berg et al. 2010; Greenwood and Jump 2014).

Conclusion

In summary, both abundance and species richness of canopy Collembola increased with elevation, and community composition changed markedly. The observed elevation-related increase in both abundance and species richness of canopy Collembola challenges previous findings and underscores the complex interplay between elevation, climate, and forest type in structuring canopy Collembola communities. Species turnover was identified as the primary driver of changes in community composition between elevations, underscoring the importance of mountain regions for biodiversity conservation. To gain a more comprehensive understanding of canopy Collembola and their interactions within forest ecosystems,

we suggest that future studies should investigate the effects of different microhabitats, incorporate seasonal dynamics and employ trait-based approaches. Finally, as climate change continues to impact ecosystems globally, a continued monitoring and better understanding of canopy arthropod dynamics will be crucial to improve conservation and sustainable management efforts in face of ongoing environmental changes.

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Authors' contributions Yunga Wu: Data curation (equal); Formal analysis (equal); Software (equal); Validation (equal); Visualization (equal); Writing – original draft (equal). Zhijing Xie: Investigation (equal); Formal analysis (equal); Writing – review & editing (equal). Zhuoma Wan: Data curation (equal); Writing – review & editing. Ting-Wen Chen: Formal analysis (equal); Writing – review & editing (equal). Qiaoqiao Ji: Writing – review & editing. Jingjing Yang: Formal analysis (equal). Donghui Wu: Conceptualization (equal); Supervision (equal); Writing – review & editing (equal). Stefan Scheu: Conceptualization (equal); Supervision (equal); Writing – review & editing (equal).

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Data Availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing interests The authors declare no competing interests.

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